THE IMPORTANCE OF BEHAVIOR IN THE RECRUITMENT OF MARINE FAUNA AND FLORA

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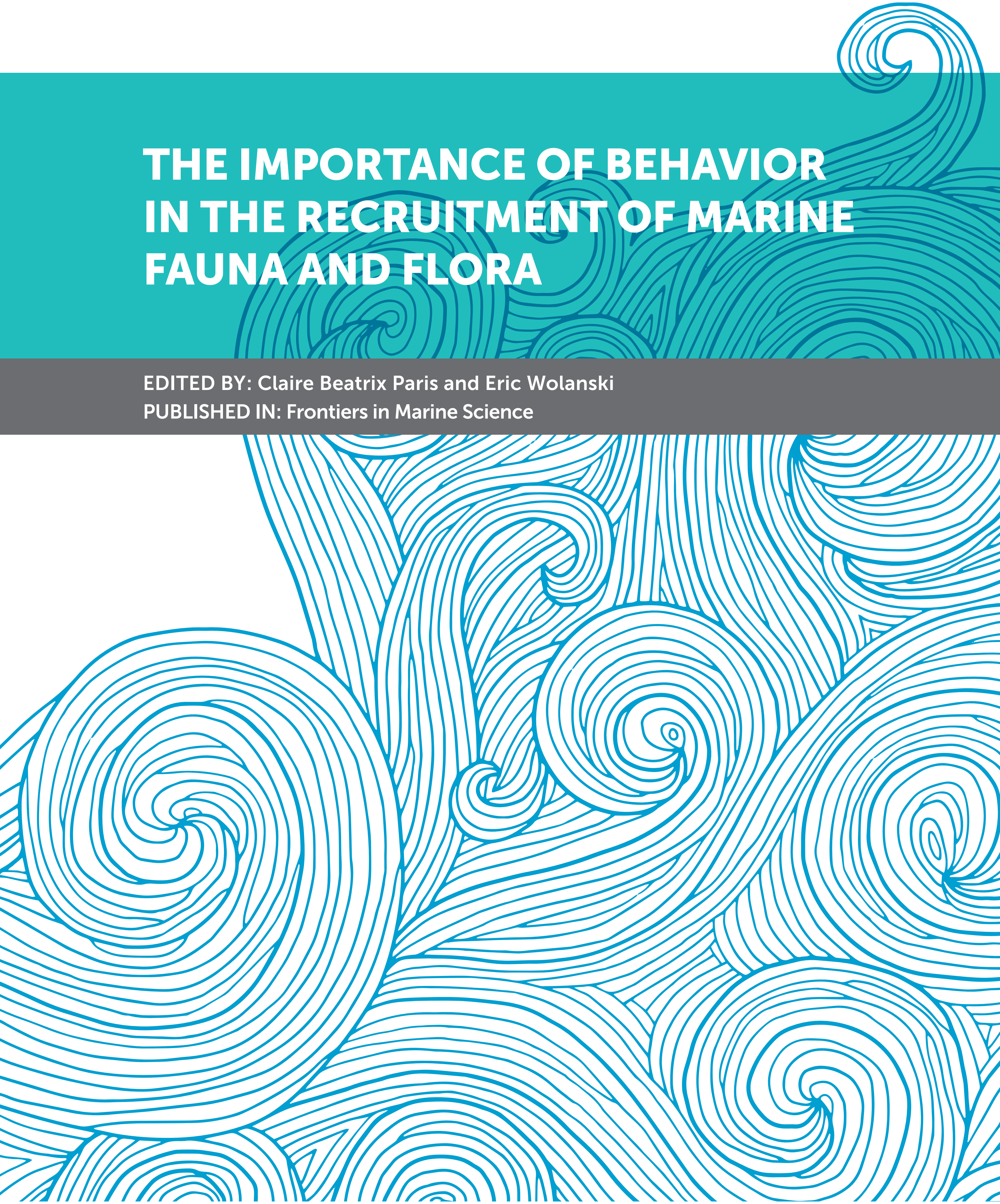

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THE IMPORTANCE OF BEHAVIOR IN THE RECRUITMENT OF MARINE FAUNA AND FLORA

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Response of Gilthead Seabream (*Sparus aurata* L., 1758) Larvae to Nursery Odor Cues as Described by a New Set of Behavioral Indexes

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Temperate marine fish larvae use a series of environmental cues (e.g., olfactory, hearing, visual) to mediate the selection of nursery habitats. However, habitat selection may vary according to individuals' physiological condition. Therefore, this study aimed to determine the ability of gilthead seabream (*Sparus aurata* L., 1758) larvae to utilize natural odor cues to locate nursery habitats along ontogeny and to examine how it varies with individual's physiological condition. The hypothesis being tested is that *S. aurata* larvae prefer coastal rocky reefs as nursery areas, but they might use coastal lagoons as nursery grounds—ecosystems known for their productivity—if under starvation conditions, as a compensatory mechanism to avoid slow growth or even death. A choice-chamber experiment was used to investigate the behavioral responses of satiated and starved laboratory-reared *S. aurata* larvae, along ontogeny (pre-flexion, flexion, post-flexion), to water collected in a coastal artificial rocky reef and a coastal lagoon. The physiological condition of *S. aurata* larvae was determined by analyzing several biochemical condition indices. Complementarily, a new set of four preference indexes were developed—Choice-Chamber Preference Indexes—and discussed to provide a clear measure of the behavioral changes of a species along ontogeny by balancing all the behavioral choices made during the experimental trials, including the unresponsive behavior. A developmental threshold was identified at 24 days post-hatching, before which insufficient swimming capability disabled responsive behavior. Beyond this threshold, post-flexion larvae preferred rocky coastal water over lagoon water, even if under starvation conditions or poor physiological condition, despite the fact that the unresponsive behavior was largely predominant. *S. aurata* larvae displayed a cautionary behavioral strategy, so the compensatory mechanisms to ensure metapopulation stability and resilience have to rely on their feeding plasticity and on being a batch-spawning species (i.e., diversified bet-hedging strategy) to compensate the lack of apparent behavioral plasticity.

Keywords: fish larvae, odor cues, ontogeny, physiological condition, habitat selection, compensatory mechanism

INTRODUCTION

The value of nursery areas relies on a series of components that set their biological relevance, namely those components pertaining to connectivity and population dynamics (connectivity, ontogenic migration, seascape migration), ecological and ecophysiological factors (ecotone effects, eco-physiological factors, food/predation trade-offs, food webs), and resource dynamics (resource availability, ontogenic diet shifts, allochthonous inputs) (Sheaves et al., 2015). Therefore, the ability of species to respond to the intrinsic complexity of this ecosystem framework is vital for them. However, the relevance of the behavioral component of marine fish larvae, hatched from pelagic eggs, on their recruitment into coastal and estuarine temperate regions has never been quantified, and most often not even recognized (see Teodósio et al., 2016 for a review). Recently, the Sense Acuity And Behavioral (SAAB) hypothesis was proposed to explain how temperate fish larvae hatched from pelagic eggs in coastal areas find and swim toward estuarine ecosystems, which they will use as nursery grounds (Teodósio et al., 2016). The first premise of this hypothesis postulates that post-flexion larvae rely on their sense acuity to locate estuarine ecosystems by detecting a suite of environmental cues (odor, sound, visual) originated in these ecosystems when they are in coastal or offshore areas (Teodósio et al., 2016). The second premise postulates that once larvae sense estuarine cues, they will swim toward an estuarine ecosystem using distinct swimming strategies which vary according to their location (offshore areas with no influence of patchy estuarine cues, offshore or nearshore areas under the effect of patchy estuarine cues, estuarine plume, or near the entrance of an estuary). Larvae may also swim toward the coast when they are offshore and away from any estuarine cue as a result of an innate behavior (Faillettaz et al., 2015; Teodósio et al., 2016).

The capacity of fish larvae to respond to environmental cues depends first on their ability to detect stimuli, and then on their swimming abilities to follow those cues (Boehlert and Mundy, 1988; Huijbers et al., 2012). Generally, sense acuity and swimming abilities increase along ontogeny (Teodósio et al., 2016); however, some species are capable of physically responding to stimuli immediately upon hatching, while others may take nearly 2 months to react to stimuli (Arvedlund and Kavanagh, 2009). Potential larval stimuli include water pressure gradients (Burke et al., 1995), magnetism (Qin et al., 2015), visual (Whitfield, 1994; Faillettaz et al., 2015), auditory (Staaterman et al., 2014), and odor-based cues (McCormick and Manassa, 2008; Arvedlund and Kavanagh, 2009), which may be used in tandem to identify suitable habitats (Lecchini et al., 2005; Hale et al., 2008). These environmental cues will then trigger a variety of larval behaviors, such as orientation (Paris et al., 2013; Faillettaz et al., 2015), vertical migration (Fortier and Leggett, 1983), predator avoidance (Lehtiniemi, 2005), and habitat selection (Gerlach et al., 2007).

Fish larvae perceive odor cues over greater distances than any other cue (Teodósio et al., 2016), and they can distinguish the chemical signatures present in the water to pinpoint the location of a nursery habitat (Atema et al., 2002; Døving et al., 2006; Paris et al., 2013). Chemical signatures are determined by abiotic or biotic factors, as type of substrate (V. Baptista, CCMAR, unpublished data), vegetation (Radford et al., 2012), or chemical signals released by conspecifics (Døving et al., 2006). However, most of the research done about habitat selection focused on coral reef fish larvae (see Teodósio et al., 2016 for a review), which suggests the existence of an olfactory-driven homing behavior (Gerlach et al., 2007). Such behavior is also relevant for the understudied temperate fish species (James et al., 2008; Radford et al., 2012), as proposed by the SAAB hypothesis (Teodósio et al., 2016).

Estuarine ecosystems are facultative nursery habitats for some of the temperate fish larvae hatching from pelagic eggs in coastal areas, despite the plentiful of resources and suitable abiotic characteristics that these ecosystems may offer to enhance larvae's growth and survival (Chaoui et al., 2006; Escalas et al., 2015). Indeed, habitat selection is the outcome of a non-random use of space, driven by environmental stimuli and behavioral choices under changing resource conditions (Kramer et al., 1997; Railsback and Harvey, 2002) and balanced by the risks inherent in each behavioral decision (Lima and Dill, 1990). Habitat choice is a mechanism resulting from a coevolutionary process allowing individuals to choose the highest quality habitat available to acquire the greatest fitness benefit (Kristan, 2003), and thus putatively enabling metapopulations with increased stability and resilience. The conditional strategy hypothesis, which states that genetically monomorphic individuals decide on tactics depending on their status (size, sex, age) or condition (energy reserves) to acquire higher fitness (Gross, 1996), frames perfectly the conundrum posed by an individual's habitat choice decisions. In the case of fish, the search for high-quality habitats depends also on density-independent (environmental variables as water temperature, salinity, oxygen concentration, light) (Craig and Crowder, 2002) and density-dependent factors (e.g., competition, predation risk, available substrate, and refuge area) (Craig and Crowder, 2002; Shepherd and Litvak, 2004). Additionally, the combination of factors leading to habitat selection may vary along ontogeny, which makes it a very dynamic process (Craig and Crowder, 2002; Kerr et al., 2010).

Under this framework, we hypothesize that fish larvae that use estuarine habitats as facultative nursery areas will ingress into such nutrient-rich habitats when in poor physiological condition, as a compensatory mechanism to avoid slow growth or even death. Thus, this study used the gilthead seabream *Sparus aurata* Linnaeus 1758 (Actinopterygii: Sparidae) larvae as a model species to determine their preference for coastal rocky reef or coastal lagoon habitats along ontogeny and at two different states of food supply (satiation and starvation). Habitat preference was quantified with a choice-chamber experiment, in which water from an artificial coastal rocky reef and a coastal lagoon were used to evaluate larvae's preference.

The evolution of gilthead seabream larvae behavioral responses were quantified along ontogeny with a new set of four preference indexes developed in this paper and named Choice-Chamber Preference Indexes (Preference Index, Minimum Consecutive Time Index, Maximum Consecutive Time Index, Overall Time Index). The development of these indexes is of prime importance because so far there is no consistent methodology to analyze data obtained with choice-chamber experiments. For example, Radford et al. (2012) present their results as the mean percentage of time larvae spent in the preferred water type, while Atema et al. (2002) and Gerlach et al. (2007) calculated a preference index that varied between −100 and +100% and calculated as the difference between the relative mean time spent in waters from two different habitats. Furthermore, and as far as we perceive them, none of these works accounted for unresponsive and inconclusive behavior (Atema et al., 2002; Gerlach et al., 2007; Radford et al., 2012). Thus, we also aim to evaluate the advantages and disadvantages of each one these indexes and their applicability to other taxa.

MATERIALS AND METHODS

Model Species: *Sparus aurata* Linnaeus 1758 (Actinopterygii: Sparidae)

Sparidae uses temperate coastal areas as preferential spawning grounds, where larvae might recruit into rocky reef areas or vegetated areas (Harmelin-Vivien et al., 1995; Borges et al., 2006; De Raedemaecker et al., 2010). Sparidae also uses estuarine ecosystems as alternative nursery areas (Chaoui et al., 2006; Abecasis and Erzini, 2008; Isnard et al., 2015), as the gilthead seabream, *S. aurata* Linnaeus, 1758 (Chaoui et al., 2006; Abecasis and Erzini, 2008; Isnard et al., 2015).

S. aurata may ingress into coastal lagoons as larvae (as early as pre-metamorphic larvae) or as juveniles during spring (Mercier et al., 2012; Tournois et al., 2013), returning to the coast during autumn (Mercier et al., 2012). Adults might re-ingress into coastal lagoons several times during their life even if they spent the juvenile phase at sea (Mercier et al., 2012). While in coastal lagoons, adults use seagrass habitats more frequently than any other type of habitat, but without exhibiting a consistent diel pattern of activity (Abecasis and Erzini, 2008). Yet, adults may exhibit a homing behavior when displaced from their home range within the lagoon (Abecasis and Erzini, 2008), but without necessarily returning to their nursery lagoon later in life (Mercier et al., 2012). *S. aurata* exhibits high trophic plasticity (i.e., incorporate organic matter with different origins—terrestrial, lagoon, marine) (Escalas et al., 2015) and feeding plasticity (Gamito et al., 2003; Tancioni et al., 2003). Some of their prey aggregate in seagrass patches, which might explain why they prefer this habitat over other coastal lagoon habitats (Abecasis and Erzini, 2008).

Experimental Design

The preference of *S. aurata* larvae for coastal and lagoon water was tested with 546 laboratory-reared larvae, of which 306 larvae and 240 larvae were tested under satiation and starvation conditions, respectively (**Table 1**). Each larva is an experimental unit assigned randomly to each treatment among those that were available at the Aquaculture Research Station of the Portuguese Institute for the Ocean and Atmosphere (Olhão, Portugal). The exogenous feeding of larvae used in this work initiated at 4 days post-hatching (DPH) and flexion occurred when larvae reached ~7 mm (24 DPH). Generally, the planktonic life duration of *S. aurata* lasts for 60–70 days (Moretti et al., 1999). Experiments were carried out in a temperature controlled room at Ramalhete Marine Station (CCMAR, University of Algarve).

TABLE 1 | Number of *Sparus aurata* larvae tested along ontogeny under satiation and starvation conditions.

Development stage	Satiation	Starvation
Pre-flexion	120	75
Flexion	20	20
Post-flexion	166	145
Total	306	240

The water types used in this experiment were collected in an artificial rocky reef (coastal jetty) in Quarteira (Portugal, 37°03′58′′ N, 8°06′13′′ W) and inside the Ria Formosa coastal lagoon (Portugal, 37°00′20′′ N, 7°57′59′′ W). Each water type was kept aerated in 70 l glass aquaria, which flowed into the choice-chamber through a peristaltic pump.

The swimming capabilities of Sparidae increase along ontogeny (Pattrick and Strydom, 2009; Faria et al., 2011), however, swimming capabilities are limited before post-flexion—for example, up to 3–4 times lower for *Pagrus aurata* (Sparidae) pre-flexion larvae (Clark et al., 2005). Indeed, a developmental threshold was identified at 24 DPH, before which insufficient swimming capability disabled responsive behavior. The flow rate was set at 20 ml min^{-1} in each choice lane (area 1 and 2 in **Figure 1**) for larvae younger than 24 DPH (i.e., pre-flexion larvae), and at 60 ml min^{-1} for larvae older than 24 DPH (i.e., flexion and post-flexion larvae). Such slow flow speeds (both <0.5 cm s^{-1}) may not have altered the behavioral response of larvae to odor cues since they were not forced to swim against the flow to hold their position in the chamber. The initial flow rate was the minimum flow rate possible to set in our choice-chamber experiment to guarantee a laminar flow in the chamber, after testing it with a food coloring dye.

Water from the two sites was collected along the course of the experiment. Water temperature was kept at 19.1 ± 1.1°C during the entire experiment, while salinity was kept constant during trials. The average salinity at the coast and coastal lagoon was 35.5 ± 1.0 and 35.9 ± 0.3, respectively. Dwarf eelgrass *Zostera noltii* (Hornemann, 1832) was added to the aquarium containing the coastal lagoon water since this seagrass is a larval settlement habitat within the Ria Formosa lagoon (Cabaço et al., 2005).

The behavioral responses of *S. aurata* larvae to the odor cues present in two water sources were tested in a choice chamber apparatus (**Figure 1**). The chamber's design was based on the one developed by Gerlach et al. (2007) and made with plexiglass (20 × 4 × 5 cm, L × W × H). The chamber features two frontal water inlets (one for each water source; see A and B in **Figure 1**) and a rear water outlet (see C in **Figure 1**). Larvae were tested along ontogeny every 2 days, from 4 to 57 DPH, to encompass all larval ontogenic stages—pre-flexion, flexion, and post-flexion. During the experimental period, larvae were fed sequentially with enriched rotifers (4 to 25 DPH), enriched *Artemia* metanauplii (15 to 30 DPH), and inert micro diet (15 to 57 DPH). Larvae

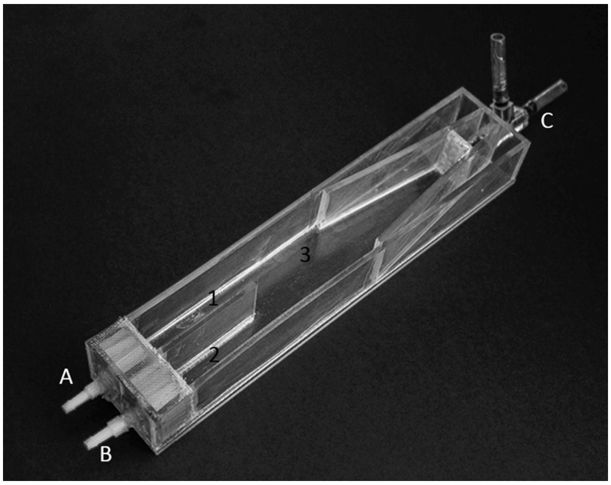

FIGURE 1 | Choice-chamber used to test the response of *Sparus aurata* larvae to odor cues along ontogeny. Legend: A, inlet hose 1; B, inlet hose 2; C, outlet hose; 1, choice-lane 1; 2, choice-lane 2; 3, area where larvae were placed at the beginning of each trial, and also the area where unresponsive behavior is assigned.

tested under starvation conditions were left without food for 2 days before trials.

For each trial, a single larva was placed in the mid-section of the choice-chamber (area 3 in **Figure 1**) and allowed to acclimatize for 2 min. Then, the position of each larva within the choice-chamber was visually tracked at every 10-s interval for 2 min. After, larva rested for 1 min, during which the position of the water inlet hoses was switched for randomization purposes. The larva was then given 2 min for acclimatization, followed by 2 min of behavioral tracking. Unresponsive behavior was assigned to larvae present in the central area of the choice-chamber at every 10-s interval (area 3 in **Figure 1**), while lagoon and coastal water preference were assigned to larvae at the corresponding lanes at every 10-s interval. This procedure follows the experimental design of Gerlach et al. (2007).

A minimum of 20 trials per trial-day was attempted; however, this was not always possible for larvae kept in starvation because some died (see **Table 1** for differences in the number of larvae tested in satiation and starved conditions). The alleged interference of the observer on the behavior of larvae during trials was minimized by maintaining the maximum distance possible while assuring a correct observation of each larva behavior. After each trial, larvae were measured (± 1 mm) under a stereomicroscope and preserved in liquid nitrogen (−196°C) for subsequent RNA and DNA analyses.

Chi-square tests (data not shown) were used to verify the behavior differences displayed by each larva to odor cues before and after switching the water sources for each lane. If the larva showed distinct behavior between trials, then this larva was assigned as unresponsive to the odor cues, and discarded from further analyses. However, if the larva showed the same behavior in both trials, then data was analyzed by combining the observations done in each trial, thus totaling 240 s. Chi-square tests were also used to test for the differences in the absolute frequencies registered between development stages (pre-flexion, flexion, post-flexion) between and within treatments (satiation, starvation).

Choice-Chamber Preference Indexes

The behavioral response of *S. aurata* larvae to olfactory stimuli along ontogeny, and under satiation and starvation conditions, was expressed by the Choice Chamber Preference Indexes: (i) Preference Index (PI), (ii) Minimum Consecutive Time (MinCT) index, (iii) Maximum Consecutive Time (MaxCT) index, (iv) Overall Time (OT) index. It is relevant to highlight that none of these indices account for the inconclusive behavior (i.e., when larvae spend the same time following each cue), whose interpretations have to be done based on its relative frequency.

The Preference Index (PI) (Equation 1) is calculated as follows:

$$PI = \left[\left(\sum t_{LW} - \sum t_{CW}\right) \times T^{-1}\right] \times \left(1 - \sum t_{UNR} \times T^{-1}\right) \tag{1}$$

where T represents the sum of both trials duration (i.e., 240 s), $\sum t_{LW}$ represents the total time larva spent exhibiting preference for lagoon water, $\sum t_{CW}$ represents the total time larva spent exhibiting preference for coastal water, and $\sum t_{UNR}$ represents the total time larvae spent exhibiting an unresponsive behavior in both trials. PI varies between –1 (coastal water preference during the entire trial) and 1 (lagoon water preference during the entire trial), while 0 indicates that larvae were unresponsive (i.e., without following an odor cue) or undecided (i.e., alternating between the two odor cues during equal period of time).

The MinCT (Equation 2) and MaxCT (Equation 3) indexes are the minimum and maximum consecutive relative time a larva spent oriented toward the preferred water type, or exhibiting an unresponsive behavior during both trials ($\mathrm{minCT}_{\mathrm{trial}\ 1\ \mathrm{v}\ 2}$; $\mathrm{maxCT}_{\mathrm{trial}\ 1\ \mathrm{v}\ 2}$—the subscript "v" represents the logical symbol "Or"). Please note that these indexes report only to data referring to the predominant behavior during trials, and are normalized by dividing the registered time by the time of one trial ($\mathrm{T}_{\mathrm{trial}}$, 120 s). For example, if a larva shows preference for lagoon water, and if the minimum time this larva spent following lagoon water was 30 s during trial 1 ($\mathrm{minCT}_{\mathrm{trial}\ 1}$) and 50 s during trial 2 ($\mathrm{minCT}_{\mathrm{trial}\ 2}$), in 120 s trials ($\mathrm{T}_{\mathrm{trial}}$), then the MinCT for this larva is 0.25 (Equation 2). The same concept applies to the MaxCT index (Equation 3).

$$\begin{aligned} MinCT &= MinCT_{trial\ 1} \times (T_{trial})^{-1}\ \ if\ minCT_{trial\ 1} \leq minCT_{trial\ 2}\ or \\ MinCT &= MinCT_{trial\ 2} \times (T_{trial})^{-1}\ \ if\ minCT_{trial\ 1} > minCT_{trial\ 2} \quad (2) \\ MaxCT &= MaxCT_{trial\ 1} \times (T_{trial})^{-1}\ \ if\ maxCT_{trial\ 1} \geq maxCT_{trial\ 2}\ or \\ MaxCT &= MaxCT_{trial\ 2} \times (T_{trial})^{-1}\ \ if\ maxCT_{trial\ 1} < maxCT_{trial\ 2} \quad (3) \end{aligned}$$

The Overall Time (OT) index is calculated for each behavioral response and larva. OT is calculated as the sum of all total non-consecutive time periods that a larva spent in each water source [$\mathrm{t}_{\mathrm{LWn}}$—n partial time periods spent following lagoon water

(LW) cues—Equation 4.1, t_{CWn}—n partial time periods spent following coastal water (CW) cues—Equation 4.2] or exhibiting an unresponsive behavior [t_{UNRn}—n partial time periods spent exhibiting unresponsive behavior (UNR)—Equation 4.3] during both trials, and normalized by the sum of both trials (T, i.e., 240 s) (Equation 4). For example, if a larva spent three periods of 10, 40, and 50 s in trials 1 and 2 (240 s total) following lagoon water, then its' OT_{LW} index is 0.42.

$$OT_{LW} = \sum_{1}^{n} t_{LWn} \times T^{-1} \tag{4.1}$$

$$OT_{CW} = \sum_{1}^{n} t_{CWn} \times T^{-1} \tag{4.2}$$

$$OT_{UNR} = \sum_{1}^{n} t_{UNRn} \times T^{-1} \tag{4.3}$$

Data for each index is grouped by development stage (pre-flexion, flexion, post-flexion) and food condition (satiation and starvation), and displayed graphically in box-n-whisker plots for accurate visualization of data—a bar-chart is not appropriate for the correct interpretation of data. Data will often be described using the average and the standard deviation as a measure of data dispersal.

A multiple comparisons test, the Kruskal-Wallis one-way analysis of variance, was used to investigate the behavioral responses of *S. aurata* to odor cues along ontogeny (pre-flexion, flexion, post-flexion) and at different states of food supply (satiation, starvation). The significance of differences between each factor level was assessed with the Holm-Sidak *post-hoc* test, which presents unadjusted *p*-values which were compared with adjusted critical levels to avoid type I errors (Glantz, 2012). It was not possible to use a parametric test because ANOVA's assumptions were not met.

Physiological Condition of *Sparus aurata* Post-flexion Larvae

Nucleic acids derived indices, as the RNA/DNA ratio, are useful indicators of the nutritional condition of marine organisms (see Chícharo and Chícharo, 2008 for a review). Individual variability, as genetic background and/or maternal effect (yolk quantity and quality), may explain why individuals with similar age, size, and under the same diet regime exhibit distinct physiological conditions. Finally, the RNA/DNA ratio informs on individuals physiological condition which is essential to interpret their behavior.

Nucleic acid concentrations of 101 and 96 post-flexion *S. aurata* larvae in satiation and starvation conditions, respectively, were quantified according to Esteves et al. (2000) and Caldarone et al. (2001). Due to tissue effects on RNA and DNA concentration, whole larvae were analyzed (Olivar et al., 2009). The methodological analysis involves mechanical and chemical homogenization of tissues and subsequent fluorescence-photometric measurements using ethidium bromide (EB) as a specific nucleic acid fluorochrome dye. Fluorescence was measured on a microplate reader (Biotek Synergy HT model SIAFRTD) using an excitation wavelength of 365 nm and an emission wavelength of 590 nm. Concentrations were determined by running standard curves of DNA-EB and RNA-EB every day with known concentrations of λ-phagus DNA (0.25 $\mu g\ \mu l^{-1}$) and 16S-23S *E. coli* RNA (4 $\mu g\ \mu l^{-1}$) (Roche), in the appropriate range of values. The average ratio of DNA and RNA slopes (mean ± SE) was 4.1 ± 0.96. The nutritional condition was assessed by the following nucleic acid derived indices: sRD, DNA/DW, and RNA/mg indexes. The RNA/DNA ratios were standardized (sRD) using this information and the reference slope ratio of 2.4, according to Caldarone et al. (2006).

The size of post-flexion larvae had no influence on their sRD ($N = 197$; $R^2 = 0.013$; $P = 0.114$). sRD ratios were converted to temperature-adjusted protein growth rates by applying the equation from Buckley (1984) and Buckley et al. (2008), considering the average water temperature during the experiment (19.1 ± 1.1°C). Thus, when larvae's protein growth rates are ≤ 0 or > 0, larvae are in poor and good nutritional condition, respectively (Robinson and Ware, 1988). In the case of our *S. aurata* larvae, the calculated sRD critical value was 0.8 (sRD ≤ 0.8—larvae in poor physiological condition; sRD > 0.8—larvae in good physiological condition). Fish larvae can be in good condition even if submitted to short-term starvation conditions, either due to genetic characteristics and/or to previously feeding history (Robinson and Ware, 1988).

The preference index was set as a dependent variable of sRD. This generates a scatterplot in which larvae are plotted in four quadrants: (i) preference for lagoon water (PI > 0) and in good physiological condition (sRD > 0.8); (ii) preference for lagoon water (PI > 0) and in poor physiological condition (sRD ≤ 0.8); (iii) preference for coastal water (PI ≤ 0) and in poor physiological condition (sRD ≤ 0.8); (iv) preference for coastal water (PI > 0) and in good physiological condition (sRD > 0.8). The differences in the frequency distribution of larvae between treatments (satiation vs. starvation) were investigated with a chi-square test, while differences in the average value of each quadrant between treatments were assessed through a *t*-test if data is normally distributed, or with the corresponding non-parametric Mann-Whitney *U*-test.

RESULTS

Overall, the response of larvae to coastal and lagoon water odor increased along ontogeny. During the pre-flexion stage, 93.3 and 100% of the larvae tested were unresponsive to odor cues under satiation (**Figure 2A**) and starvation conditions (**Figure 2B**), respectively. Unresponsive behavior decreased to a minimum of 39.8% for larvae at the post-flexion stage under satiation conditions (**Figure 2B**). Larvae tended to prefer coastal water in detriment of lagoon water during flexion and post-flexion development stages, either at satiation or starvation conditions. The smallest and biggest difference between the preference for coastal and lagoon water was observed while larvae were at the flexion stage. The maximum difference was 35.0% that was observed under satiation conditions (**Figure 2A**), while the minimum difference was 5.0% and observed under starvation conditions (**Figure 2B**). The inconclusive behavior accounted for 5.4 and 7.6% of satiated and starved post-flexion larvae, respectively (**Figure 2**). Overall, significant differences were

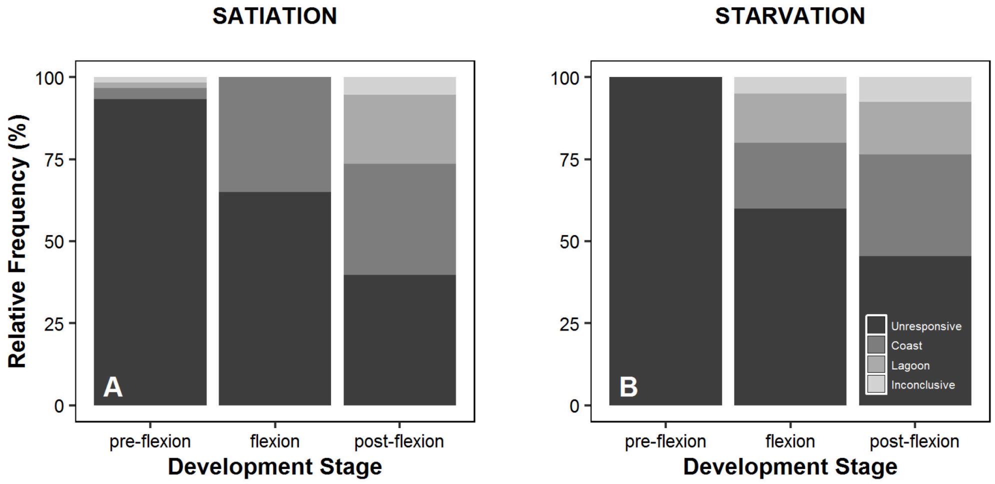

FIGURE 2 | Behavior exhibited by *Sparus aurata* larvae (unresponsive to water cues, coastal water preference, lagoon water preference, inconclusive behavior) during choice-chamber trials performed along ontogeny (pre-flexion, flexion, post-flexion) and in satiation **(A)** and starvation **(B)** conditions.

found in the absolute frequencies observed between all levels (pre-flexion, flexion, post-flexion) within treatments (satiation and starvation) (χ^2 test, $p = 0.000$), and for the level pre-flexion between treatments (χ^2 test, $p = 0.000$) (**Table 2**).

The preference index varied between −1.0 and 1.0, and averaged between −0.18 ± 0.32 (satiation, flexion larvae) and 0.0 ± 0.0 (starvation, pre-flexion larvae), which shows a slight preference toward coastal water (**Figure 3**). There were no significant differences between larvae at satiation and starvation conditions at any level of development stage (unadjusted $P > 0.05$) (**Table 3**). The only significant difference was observed between pre-flexion and flexion larvae at satiation conditions (unadjusted $P = 0.013$) (**Table 3**).

The MinCT and MaxCT indices must be evaluated in conjunction with the number of observations made for each behavior type at a given development stage, to assure statistical significance. Thus, data on MinCT and MaxCT will be used only to access the behavior of larvae along ontogeny regarding the time spent performing an unresponsive behavior, and comparing behaviors at the post-flexion stage.

The average MinCT for unresponsive larvae varied between 65 ± 38 s (flexion at satiation conditions) and 120 ± 0 s (pre-flexion at starvation conditions) (**Figures 4A,B**). The MinCT index for unresponsive larvae did not vary significantly between larvae at satiation and starvation conditions within each development stage ($0.196 <$ Unadjusted $P < 0.738$), but it varied significantly between pre-flexion and flexion larvae (unadjusted $P < 0.001$) and pre-flexion and post-flexion larvae (unadjusted $P< 0.001$) in the comparison "Development stage," "Development stage within larvae at satiation conditions," and "Development stage within larvae at starvation conditions" (**Table 4**). For those larvae at post-flexion, the MinCT index did not vary significantly between larvae at starvation and satiation conditions within each behavioral response ($0.107 <$ unadjusted $P < 0.790$), but it varied significantly between those larvae exhibiting unresponsive behavior and coastal water preference (unadjusted $P< 0.001$) and unresponsive behavior and lagoon water preference (unadjusted $P = 0.002$) (**Table 5**).

TABLE 2 | Significance level of the comparisons calculated with a Chi-square test for the absolute frequencies registered for the behavior exhibited by *Sparus aurata* larvae (unresponsive to water cues, coastal water preference, lagoon water preference, inconclusive behavior) during choice-chamber trials performed along ontogeny (pre-flexion, flexion, post-flexion) and in satiation and starvation conditions.

Comparisons	*p*
SAME DEVELOPMENT STAGE BETWEEN CONDITIONS	
Pre-flexion*	0.000
Flexion	0.096
Post-flexion	0.081
DEVELOPMENT STAGES WITHIN SATIATION	
Pre-flexion vs. flexion*	0.000
Flexion vs. post-flexion*	0.000
Pre-flexion vs. post-flexion*	0.000
DEVELOPMENT STAGES WITHIN STARVATION	
Pre-flexion vs. flexion*	0.000
Pre-flexion vs. post-flexion*	0.000
Flexion vs. post-flexion*	0.000

The asterisk (*) highlights the existence of significant differences.

The average MaxCT for unresponsive larvae varied between 101 ± 23 s (flexion at starvation conditions) and 120 ± 0 s (pre-flexion at starvation conditions) (**Figures 4C,D**). The MaxCT index for unresponsive larvae did not vary significantly between larvae at satiation and starvation conditions within each development stage (unadjusted $P > 0.05$), except for larvae at flexion (unadjusted $P= 0.044$), but this index varied significantly between larvae at different development stages

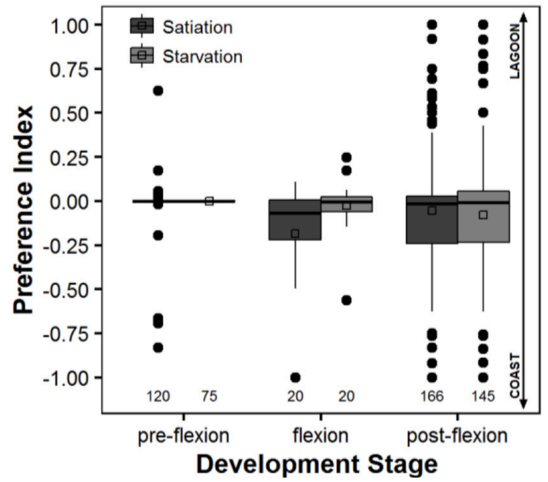

FIGURE 3 | Box-n-whiskers plots representing the Preference Index determined for *Sparus aurata* larvae under satiation and starvation conditions along their ontogeny. Negative values of this index indicate a preference for coastal water, while positive values indicate a preference for lagoon water. The plot depicts the 1st and 3rd quartiles, median, mean, and outliers, as well as the 5th and 95th percentiles as the minimum and maximum whiskers, respectively. Legend: open squares represent the mean; thick black line represents the median; full black circles represent the outliers; the numbers at the bottom of the graph account for the number of observations made.

TABLE 3 | Multiple comparisons' statistical output for the Preference Index.

Comparisons	Diff. of Means	*t*	Unadjusted *P*	Critical level
CONDITION				
Satiation vs. starvation	11.537	1.369	0.172	0.050
CONDITION WITHIN EACH DEVELOPMENT STAGE				
Pre-flexion	2.882	0.284	0.776	0.050
Flexion	37.750	1.732	0.084	0.050
Post-flexion	6.021	0.769	0.442	0.050
DEVELOPMENT STAGE				
Pre-flexion vs. flexion	23.851	1.985	0.048	0.025
Pre-flexion vs. post-flexion	14.609	2.280	0.023	0.017
Flexion vs. post-flexion	9.242	0.798	0.425	0.050
DEVELOPMENT STAGE WITHIN LARVAE AT SATIATION CONDITIONS				
Pre-flexion vs. flexion*	41.285	2.481	0.013	0.017
Flexion vs. post-flexion	31.127	1.909	0.057	0.025
Pre-flexion vs. post-flexion	10.158	1.230	0.219	0.050
DEVELOPMENT STAGE WITHIN LARVAE AT STARVATION CONDITIONS				
Pre-flexion vs. flexion	6.417	0.370	0.711	0.050
Pre-flexion vs. post-flexion	19.060	1.945	0.052	0.017
Flexion vs. post-flexion	12.644	0.769	0.442	0.025

The post-hoc Holm-Sidak test was used to access the statistical significance of the comparisons made for the factors condition and development stage. The asterisk (*) highlights the existence of significant differences.

($<0.001 <$ unadjusted $P < 0.021$) (**Table 6**). For those larvae at post-flexion, the MaxCT index did not vary significantly between larvae at starvation and satiation conditions within each behavioral response ($0.282 <$ unadjusted $P < 0.811$), but it varied significantly between those larvae exhibiting unresponsive behavior and coastal water preference (unadjusted $P< 0.001$) and unresponsive behavior and lagoon water preference (unadjusted $P = 0.014$) (**Table 7**).

The overall time that larvae spent exhibiting an unresponsive behavior decreased along ontogeny development, from 240.0 ± 0.0 s (pre-flexion, starvation) (**Figure 5B**) to 106.0 ± 76.8 s (post-flexion, satiation) (**Figure 5A**). In contrast, the time spent following the odor cues from coastal and lagoon water increased.

The average standard RNA:DNA ratio (sRD) of satiated ($n = 101$; 0.51 ± 0.25) and starved ($n = 96$; 0.50 ± 0.25) post-flexion larvae did not differed significantly (U-test, $p = 0.941$) (**Figure 6**). The distribution of larvae among the four quadrants – combination of lagoon ($PI > 0$) and coastal ($PI \leq 0$) preference vs. above and below the 0.8 critical level—is non-significantly different for satiated and starved larvae (χ^2 test, $p = 0.17$), as well as the average sRD and PI values within each quadrant ($p > 0.05$, t-test) (**Figure 6**).

DISCUSSION

Considerations about the Choice-Chamber Preference Indexes

The Preference Index has two main advantages. First, it aims to provide a uniform methodology enabling researchers to compare data between species and at distinct development stages, even if data were obtained using different experimental designs (particularly the time length of experimental trials). The second advantage, and probably the most important, is that the Preference Index provides a clear measure of the behavioral changes of a species along ontogeny (or any other grouping factor–sex, habitat, pCO_2) by balancing all the behavioral choices made during the experimental trials, including the unresponsive behavior. We advocate that unresponsive behavior should be included in the calculation of a preference index since its exclusion overestimates, the preference of a certain species for a given habitat, even if slightly. Also, the assignment of a behavioral choice to areas outside the choice lanes is prone to bias since the mixture of water from two different sources in this area does not have to be necessarily uniform at all times.

The MinCT and MaxCT Indexes complement the information provided by the Preference Index. In the particular case of our study, where the Preference Index only suggests that flexion and post-flexion larvae have a slight preference for coastal habitats, these MinCT and MaxCT indexes demonstrate that the unresponsive behavior diminished along ontogeny. This fact is especially evident for the MinCT index, however for other species or the same species but if tested at subsequent life stages, the maximum time spent exhibiting unresponsive behavior would decrease and reveal even more the usefulness of the MaxCT index. The Overall Time (OT) index did not exhibit the constraints shown by the MaxCT index for *S. aurata* larvae since it clearly captured the decrease of the unresponsive behavior, and also the effect of starvation on larvae's behavior.

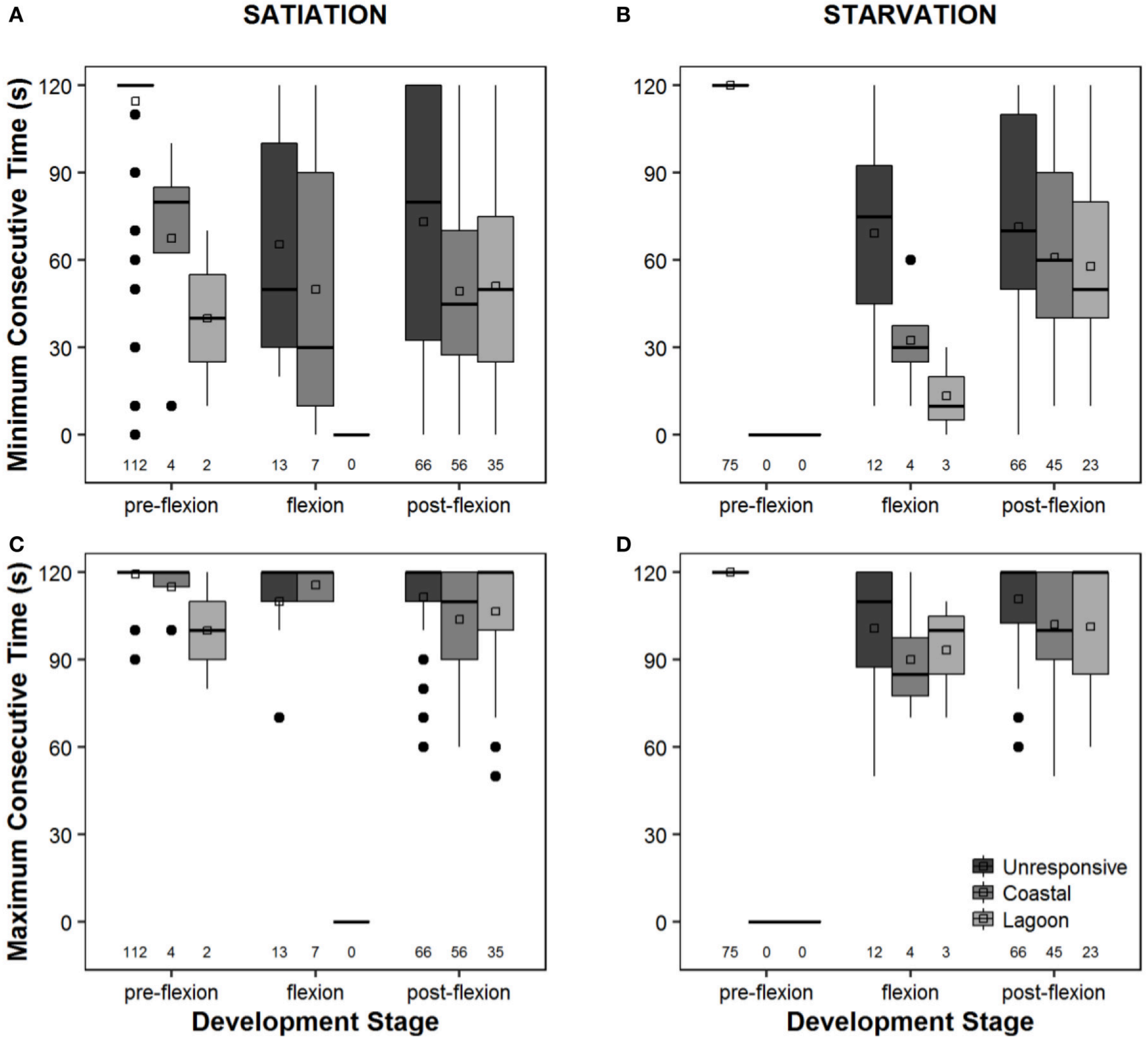

FIGURE 4 | Box-n-whiskers plots representing the minimum **(A,B)** and maximum **(C,D)** consecutive time (seconds) that *Sparus aurata* larvae spent exhibiting a given behavior (unresponsive, or preference for coastal or lagoon water), during choice-chamber trials performed along ontogeny (pre-flexion, flexion, post-flexion) and in satiation **(A,C)** and starvation **(B,D)** conditions. The behavior of each larva was assigned after two choice-chamber trials, and those larvae with inconclusive behavior were not considered in these analyses. The plot depicts the 1st and 3rd quartiles, median, mean, and outliers, as well as the 5th and 95th percentiles as the minimum and maximum whiskers, respectively. Legend: open squares represent the mean; thick black line represents the median; full black circles represent the outliers; the numbers at the bottom of the graph account for the number of observations made.

Finally, the Choice Chamber Preference Indexes also have the potential to be important contributors for parameterizing the behavioral responses of fish larvae in lagrangian behavioral models. However, these indexes should be used cautiously when the inconclusive behavior is predominant—which was not the case in our study. In such situations, the information obtained from the frequency of each behavior (as displayed in **Figure 2**) should be preferentially used for the interpretation of larvae behavior and in parameterizing lagrangian models, since the indexes do not account for inconclusive behavior.

Response of *Sparus aurata* Larvae to Odor Cues

The response of *S. aurata* larvae to nursery odor cues increased along ontogeny, thus coinciding with the development of olfactory structures and increased swimming abilities (up to 19.3 cm s^{-1}, 20.2 body lengths s^{-1}, Faria et al., 2011), as proposed by the SAAB hypothesis (Teodósio et al., 2016). The absence of pre-flexion and flexion larvae response to odor cues can be due to their incapacity to swim toward the cues, to sensing incapacity, and/or because their attraction to nursery grounds develop later during the ontogeny closer to settlement. Certainly, immunohistochemistry studies focusing on the development of

TABLE 4 | Multiple comparisons' statistical output for the Minimum Consecutive Time (MinCT) index calculated for all larvae exhibiting an unresponsive behavior.

Comparisons	Diff. of Means	*t*	Unadjusted *P*	Critical level
CONDITION				
Satiation vs. starvation	2.550	0.579	0.563	0.050
CONDITION WITHIN EACH DEVELOPMENT STAGE				
Pre-flexion	5.536	1.295	0.196	0.050
Flexion	3.782	0.330	0.742	0.050
Post-flexion	1.667	0.334	0.738	0.050
DEVELOPMENT STAGE				
Pre-flexion vs. flexion*	49.957	8.163	<0.001	0.025
Pre-flexion vs. post-flexion*	44.884	13.666	<0.001	0.017
Flexion vs. post-flexion	5.073	0.811	0.418	0.050
DEVELOPMENT STAGE WITHIN LARVAE AT SATIATION CONDITIONS				
Pre-flexion vs. flexion*	49.080	5.846	<0.001	0.025
Pre-flexion vs. post-flexion*	41.282	9.285	<0.001	0.017
Flexion vs. post-flexion	7.797	0.897	0.370	0.050
DEVELOPMENT STAGE WITHIN LARVAE AT STARVATION CONDITIONS				
Pre-flexion vs. flexion*	50.833	5.706	<0.001	0.025
Pre-flexion vs. post-flexion*	48.485	10.027	<0.001	0.017
Flexion vs. post-flexion	2.348	0.261	0.794	0.050

The post-hoc Holm-Sidak test was used to access the statistical significance of the comparisons made for the factors condition and development stage. The asterisk (*) highlights the existence of significant differences.

TABLE 5 | Multiple comparisons' statistical output for the Minimum Consecutive Time (MinCT) index calculated for all post-flexion larvae.

Comparisons	Diff. of Means	*t*	Unadjusted *P*	Critical level
CONDITION				
Satiation vs. starvation	5.540	1.228	0.220	0.050
CONDITION WITHIN EACH BEHAVIORAL RESPONSE				
Unresponsive	1.667	0.267	0.790	0.050
Coast	11.603	1.616	0.107	0.050
Lagoon	6.683	0.694	0.488	0.050
BEHAVIORAL RESPONSE				
Unresponsive vs. coast*	17.261	3.628	<0.001	0.017
Unresponsive vs. lagoon*	17.864	3.114	0.002	0.025
Coast vs. lagoon	0.603	0.100	0.920	0.050
BEHAVIORAL RESPONSE OF LARVAE AT SATIATION CONDITIONS				
Unresponsive vs. coast*	23.896	3.667	<0.001	0.017
Unresponsive vs. lagoon*	22.039	2.939	0.004	0.025
Coast vs. lagoon	1.857	0.240	0.810	0.050
BEHAVIORAL RESPONSE OF LARVAE AT STARVATION CONDITIONS				
Unresponsive vs. coast	10.626	1.533	0.126	0.025
Unresponsive vs. lagoon	13.689	1.576	0.116	0.017
Coast vs. lagoon	3.063	0.333	0.739	0.050

The post-hoc Holm-Sidak test was used to access the statistical significance of the comparisons made for the factors condition and response. The asterisk (*) highlights the existence of significant differences.

odor receptor cells along temperate fish larvae ontogeny will shed light on this issue.

Contrary to our hypothesis, post-flexion larvae did not follow the odor cues from a coastal lagoon (i.e., an alternative nursery area) as a compensatory mechanism to minimize the detrimental effects of starvation on growth and survival. Two hypotheses might have contributed to this outcome.

First, hatchery-reared larvae might have a different response behavior to odor cues than wild larvae. However, in a similar experiment, hatchery-reared larvae preferred seagrass habitat water in detriment of other water types (Radford et al., 2012). The capture of wild larvae in different stages of larval development and controlled conditions of food availability would be impossible given our experimental design. For example, a work using wild larvae in a choice-chamber experiment tested 37 larvae (James et al., 2008), while we tested 546 larvae. In this experiment, larvae preferred estuarine waters, in detriment of coastal water (James et al., 2008). However, it is important to highlight that these two studies did not consider the unresponsive behavior of larvae in their tests which is a trait that cannot be neglected in animal behavior studies.

A second hypothesis concerns with a putative necessity to exist a combination of odor cues, signaling the habitat (i.e., seagrass odor cues) and the presence of prey, and not just the habitat itself. This hypothesis deserves being investigated in future works and was suggested to explain the unresponsive behavior of *S. aurata* larvae in following the odor cues of another seagrass species signaling a nursery habitat in the Mediterranean Sea (Díaz-Gil et al., 2017). In future studies, it would also be interesting to include offshore and conspecific cues, as well as different temperature and salinity conditions, to rank larvae's preferences among different cues.

The facultative behavior of *S. aurata* in using coastal lagoons as nursery habitats for larvae, as observed in the Mediterranean Sea (Mercier et al., 2012; Tournois et al., 2013), confirms previous observations made in the Ria Formosa lagoon. The larvae of Sparidae were among the most abundant in this lagoon, and most of these larvae were post-flexion larvae collected during flood tides (Chícharo and Teodósio, 1991). So, the absence of a meaningful number of pre-flexion larvae and the presence of post-flexion larvae during flood tides suggests that spawning does not occur inside the lagoon, as observed for other species in an estuary located nearby (Faria et al., 2006; Morais et al., 2009). Larvae's ingress mechanisms were never evaluated, so larvae's ingress could result from purely stochastic events (e.g., winds, tides) (Hare et al., 2005; Schieler et al., 2014) or due to active ingress strategies (e.g., selective tidal stream transport, bottom-inflow ingress, or ingress near the bottom or margins where water velocity is slower) which include ingress during flood tides (Hare et al., 2005). However, if *S. aurata* larvae would employ active ingress strategies then larvae would likely use active retention strategies and their abundance would build-up in the lagoon, but this was not observed. The abundance of larvae was almost 900 times higher during the high-tide than during the low-tide (Chícharo and Teodósio, 1991). So, these observations

TABLE 6 | Multiple comparisons' statistical output for the Maximum Consecutive Time (MaxCT) index calculated for all larvae exhibiting an unresponsive behavior.

Comparisons	Diff. of Means	*t*	Unadjusted *P*	Critical level
CONDITION				
Satiation vs. starvation	3.100	1.778	0.076	0.050
CONDITION WITHIN EACH DEVELOPMENT STAGE				
Pre-flexion	0.625	0.369	0.712	0.050
Flexion*	9.167	2.019	0.044	0.050
Post-flexion	0.758	0.384	0.701	0.050
DEVELOPMENT STAGE				
Pre-flexion vs. flexion*	14.271	5.892	<0.001	0.025
Pre-flexion vs. post-flexion*	8.551	6.578	<0.001	0.017
Flexion vs. post-flexion*	5.720	2.311	0.021	0.050
DEVELOPMENT STAGE WITHIN LARVAE AT SATIATION CONDITIONS				
Pre-flexion vs. flexion*	9.375	2.822	0.005	0.025
Pre-flexion vs. post-flexion*	7.860	4.467	<0.001	0.017
Flexion vs. post-flexion	1.515	0.440	0.660	0.050
DEVELOPMENT STAGE WITHIN LARVAE AT STARVATION CONDITIONS				
Pre-flexion vs. flexion*	19.167	5.437	<0.001	0.017
Pre-flexion vs. post-flexion*	9.242	4.829	<0.001	0.025
Flexion vs. post-flexion*	9.924	2.789	0.006	0.050

The post-hoc Holm-Sidak test was used to access the statistical significance of the comparisons made for the factors condition and development stage. The asterisk (*) highlights the existence of significant differences.

TABLE 7 | Multiple comparisons' statistical output for the Maximum Consecutive Time (MaxCT) index calculated for all post-flexion larvae.

Comparisons	Diff. of Means	*t*	Unadjusted *P*	Critical level
CONDITION				
Satiation vs. starvation	2.592	1.132	0.259	0.050
CONDITION WITHIN EACH BEHAVIORAL RESPONSE				
Unresponsive	0.758	0.239	0.811	0.050
Coast	1.750	0.480	0.631	0.050
Lagoon	5.267	1.078	0.282	0.050
BEHAVIORAL RESPONSE				
Unresponsive vs. coast*	8.261	3.422	< 0.001	0.017
Unresponsive vs. lagoon*	7.198	2.473	0.014	0.025
Coast vs. lagoon	1.063	0.349	0.727	0.050
BEHAVIORAL RESPONSE OF LARVAE AT SATIATION CONDITIONS				
Unresponsive vs. coast	7.765	2.348	0.020	0.017
Unresponsive vs. lagoon	4.944	1.299	0.195	0.025
Coast vs. lagoon	2.821	0.719	0.472	0.050
BEHAVIORAL RESPONSE OF LARVAE AT STARVATION CONDITIONS				
Unresponsive vs. coast*	8.758	2.489	0.013	0.017
Unresponsive vs. lagoon	9.453	2.145	0.033	0.025
Coast vs. lagoon	0.696	0.149	0.882	0.050

The post-hoc Holm-Sidak test was used to access the statistical significance of the comparisons made for the factors condition and response. The asterisk (*) highlights the existence of significant differences.

suggest a passive ingress of *S. aurata* larvae into the Ria Formosa lagoon.

The decision of *S. aurata* post-larvae to adjust to new contexts (e.g., migrate or explore new habitats in the face of reducing prey availability or presence of a predator—Chapman et al., 2011; Killen et al., 2012), can also depend on individual's personality (i.e., shy or bold). Individuals can deal with uncertainty in three ways: (1) reduce uncertainty by gathering information; (2) use a strategic behavior according to the options available (state-dependent) which will produce distinct levels of reward (i.e., variance-sensitivity), (3) invest in insurance to mitigate the consequences of uncertainty (Mathot et al., 2012). In the case of *S. aurata* post-flexion larvae, it seems that they prefer insurance (i.e., unresponsive behavior, preference for coastal water) rather than mitigate the effect of starvation with uncertainty (i.e., swim toward lagoon water). Therefore, *S. aurata* ought to employ other compensatory mechanisms to mitigate the effect of starvation on metapopulation stability and resilience.

Coastal fish larvae can rely, for example, on high feeding plasticity to avoid prey mismatch (Morote et al., 2010; Chícharo et al., 2012), while batch spawning (i.e., multiple spawning events along the spawning season) would compensate for prey mismatch or other biotic and abiotic detrimental conditions (Helfman et al., 2009). In essence, this conundrum fits within the scope of the bet-hedging theory (Helfman et al., 2009). This theory is an evolutionary hypothesis proposing that individuals "optimize fitness in varying and unpredictable environments by sacrificing mean fitness to decrease variation in fitness" which can concern to any life history stage and not only with a trade-off between the survival of adults and reproduction (Olofsson et al., 2009). Bet-hedging has several strategies, the conservative bet-hedging, the diversified bet-hedging, the adaptative bet-hedging, and the dynamic bet-hedging (Crean and Marshall, 2009; Olofsson et al., 2009). The dynamic bet-hedging stipulates that when environmental conditions are unpredictable, as conditions at sea most of the time, mothers will invest in offspring phenotypic plasticity (Crean and Marshall, 2009). However, in the case of *S. aurata*, it seems that larvae's lack of behavioral plasticity precludes the existence of other strategy or strategies. Probably, *S. aurata* use a diversified bet-hedging strategy ("don't put all eggs in one basket") (*sensu* Olofsson et al., 2009) through a protracted reproduction period (i.e., batch spawning), to compensate the lack of larvae's behavioral plasticity regarding using another nursery area to compensate poor physiological condition and prey mismatch (i.e., lack of food). Therefore, the dynamics of the different bet-hedging strategies used by coastal fish, and how it influences their fitness and metapopulation stability and resilience is far from being understood, which turns this topic prone to new research and debate.

ETHICS STATEMENT

CCMAR facilities and their staff are certified to house and conduct experiments with live animals ("group-1" license by the Veterinary General Directorate, Ministry of Agriculture, Rural

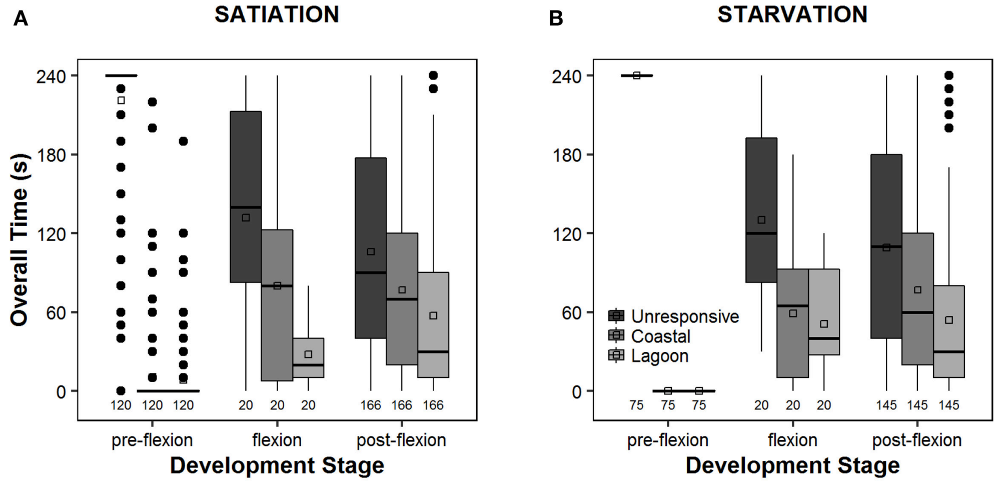

FIGURE 5 | Box-n-whiskers plots representing the non-consecutive overall time (seconds) that *Sparus aurata* larvae spent exhibiting a given behavior (unresponsive, or preference for coastal or lagoon water), during choice-chamber trials, performed along ontogeny (pre-flexion, flexion, post-flexion) and in satiation **(A)** and starvation **(B)** conditions. The behavior of each larva was assigned after two choice-chamber trials, and those larvae with inconclusive behavior were not considered in these analyses. The plot depicts the 1st and 3rd quartiles, median, mean and outliers, as well as the 5th and 95th percentiles as the minimum and maximum whiskers, respectively. Legend: open squares represent the mean; thick black line represents the median; full black circles represent the outliers; the numbers at the bottom of the graph account for the number of observations made.

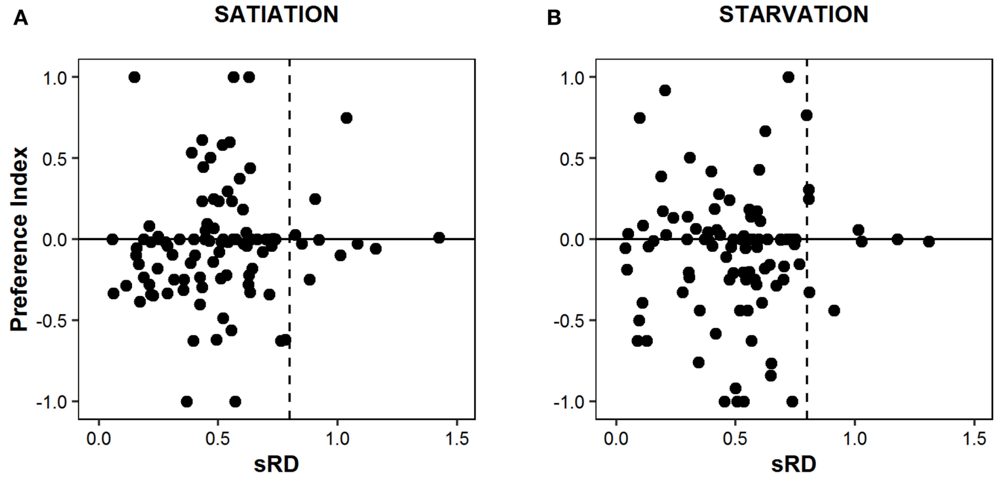

FIGURE 6 | Variability of *Sparus aurata* post-flexion larvae Preference Index (PI) in function of their standard RNA:DNA ratio (sRD) at satiation **(A)** and starvation **(B)** conditions. Negative values of the Preference Index indicate a preference for coastal water, while positive values indicate a preference for lagoon water. The vertical dashed line represents the 0.8 sRD critical level determined for gilthead seabream larvae using the equations of Buckley (1984) and Buckley et al. (2008).

Development and Fisheries of Portugal) in accordance with the three "R" policy and national and European legislation.

AUTHOR CONTRIBUTIONS

MT and PM conceived the study. LR and PP provided the fish larvae used in this study. MP performed the fish behavior tests. MP, VB, MT, and PM performed the biochemical analyses. PM, MT, and MP analyzed the data. PM and MP wrote the paper. All authors revised the paper.

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REVIEW
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Paradigm Lost: Ocean Acidification Will Overturn the Concept of Larval-Fish Biophysical Dispersal

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Most marine ecologists have in the past 25 years changed from supporting a passive-dispersal paradigm for larval marine fishes to supporting a biophysical-dispersal paradigm wherein the behaviour of larvae plays a central role. Research shows larvae of demersal perciform fishes have considerable swimming and orientation abilities over a major portion of their pelagic larval duration. These abilities depend on sensory function, and some recent research has indicated anthropogenic acidification of the oceans will by the end of the century result in sensory dysfunction. This could strongly alter the ability of fish larvae to orientate in the pelagic environment, to locate suitable settlement habitat, to bet-hedge, and to colonize new locations. This paper evaluates the available publications on the effects of acidification on senses and behaviours relevant to dispersal of fish early life-history stages. A large majority of studies tested CO_2 values predicted for the middle to end of the century. Larvae of fourteen families—all but two perciform—were studied. However, half of studies used Damselfishes (Pomacentridae), and except for swimming, most studies used settlement-stage larvae or later stages. In spite of these taxonomic and ontogenetic restrictions, all but two studies on sensory function (chemosensation, hearing, vision, detection of estuarine cues) found deleterious effects from acidification. The four studies on lateralization and settlement timing all found deleterious effects from acidification. No clear effect of acidification on swimming ability was found. If fish larvae cannot orientate due to sensory dysfunction, their dispersal will, in effect, conform to the passive dispersal paradigm. Modelling incorporating larval behaviour derived from empirical studies indicates that relative to active larvae, passive larvae will have less self-recruitment, higher median and mean dispersal distances, and lower settlement rates: further, bet hedging and colonization of new locations will decrease. The biophysical dispersal paradigm will be lost in theory and in fact, which is predicted to result in lower recruitment and less bet hedging for demersal, perciform fishes. More research is required to determine if the larvae of other Orders will be effected in the same way, or if warm- and cold-water fish faunas will be similarly effected.

Keywords: fish, larva, dispersal, sensory ability, CO_2, acidification, behaviour, connectivity

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INTRODUCTION

Most marine bony fishes have a pelagic larval stage that differs morphologically from the adult (Moser, 1981) and that is, at least potentially, dispersive. Especially for demersal fish species in the tropics, adults are often relatively site attached, and dispersal by the larvae determines the spatial scale of population connectivity (Sale, 1980, 1991). Although there are reasons to expect larval dispersal to differ between low and high latitudes (Hunt von Herbing, 2002), there is little evidence that it does. Further, making latitudinal comparisons in dispersal metrics and the factors that determine dispersal outcomes is difficult due to a variety of factors including very large differences in the taxonomic composition of marine fish communities with latitude (Leis et al., 2013). Marine fish larvae spend weeks to months in pelagic open waters away from demersal adult habitat (Luiz et al., 2013) before they must find suitable habit into which to settle. Settlement is often, but not always, associated with abrupt metamorphosis, but regardless of morphological changes, an animal that has experienced nothing but a pelagic environment must quickly adapt to a very different demersal habitat (Leis, 1991).

Traditionally, marine biologists assumed that dispersal of fish larvae is essentially a passive process, with movement of the presumed weakly-swimming larvae totally determined by currents (Roberts, 1997). More recently, swimming, orientation, behavioural, and sensory capabilities of larval marine perciform fishes have been shown to be remarkably strong for much of the pelagic larval duration, or PLD (Leis, 2006, 2010). Larvae can swim in an orientated way at speeds that are often comparable to the currents of the waters in which they live, thus directly influencing their dispersal. Larvae can detect and respond to a range of olfactory, auditory, and visual cues from settlement habitat, from within the pelagic environment (Leis et al., 2011b) and even to celestial (Mouritsen et al., 2013; Leis et al., 2014) and magnetic (Bottesch et al., 2016; O'Connor and Muheim, 2017) cues. By controlling their vertical distribution, larvae may indirectly influence their dispersal because current velocities often vary with depth. The proper functioning of the sense organs of fish larvae is essential in all these processes. As a result of these findings, the passive dispersal paradigm in larval marine fishes has been widely rejected in favour of a biophysical dispersal paradigm that recognizes the strong influence of biological factors, including behaviour of larvae, on dispersal outcomes (Leis, 2015).

As part of this paradigm shift our view of the spatial scale of larval dispersal and population connectivity has altered. Previously, marine ecologists considered populations of demersal marine fishes to be genetically and demographically open (Roberts, 1997)—that is, the new recruits to a given area did not result from propagules produced there, but from larvae that drifted passively with the currents from elsewhere. We now know that most demersal marine fish populations are closed to a greater or lesser extent (Jones et al., 2009), and that this "self-recruitment" is the result of biophysical processes, including behaviour of the larvae themselves (Leis, 2015). Nevertheless, a proportion of the larvae produced in any area are also exported to other areas. These conclusions are supported by modelling that takes into account empirically demonstrated larval-fish behaviour, e.g., Wolanski and Kingsford (2014).

The effects of lower pH as human-produced CO_2 is absorbed by the ocean have received increasing attention, and will perhaps be more profound and less spatially variable than those of the predicted increase in temperature. Acidification can affect dispersal of fish larvae in two ways. It can cause developmental errors that lead to morphological deformities, and damage to organs, including sense organs that may impair their function. Acidification also results in neurotransmitter dysfunction (Nilsson et al., 2012), and as shown in a number of studies, this interferes with the ability of fish larvae to use the sensory systems that are vital to orientation in the ocean. Without orientation ability, swimming by larvae will have greatly diminished net influence on dispersal. It is likely depth selection ability of larvae will also be diminished, resulting in less structured vertical distributions. This has important implications for dispersal outcomes. It is also possible acidification may affect other behaviours, such as swimming ability, that influence dispersal outcomes (Nagelkerken and Munday, 2016).

Studies on fish-larvae behaviour, particularly *in situ* studies, routinely find statistically significant relationships between, for example, swimming speed or depth and size of the larvae but there is always a high level of variability associated with the relationships (**Figures 1A,B**, see Leis, 2006, 2010). Some individual larvae have a more meandering swimming path through the ocean than others and will therefore pass over different demersal habitat, and have a slower start-to-finish net swim speed than more directional swimmers (**Figure 1C**). Similarly, fish larvae often have significant among-individual (within-species) swimming directionality, but there are invariably many individuals that swim in directions other than the overall mean (**Figure 1D**). These variations mean that a greater or lesser proportion of individuals will have different dispersal outcomes than the majority. This minority with different dispersal outcomes due to differences in behaviour can be regarded as contributing to bet-hedging and to colonizing new localities as, at the end of their PLD, they will be at different locations than the majority, either in direction or distance from their point of origin. Theoretical considerations commonly cite bet hedging and colonization of new localities as reasons for the evolution of a bipartite life history with a pelagic larval dispersal stage.

EVALUATION OF LITERATURE ON EFFECTS OF ACIDIFICATION ON LARVAL DISPERSAL

The present paper evaluates the evidence relating to adverse effects of acidification on behaviour of fish larvae and the function of their sensory systems relevant to orientation and dispersal, and discusses implications for larval dispersal and the implications of this for populations of demersal marine fishes, especially those of lower latitudes.

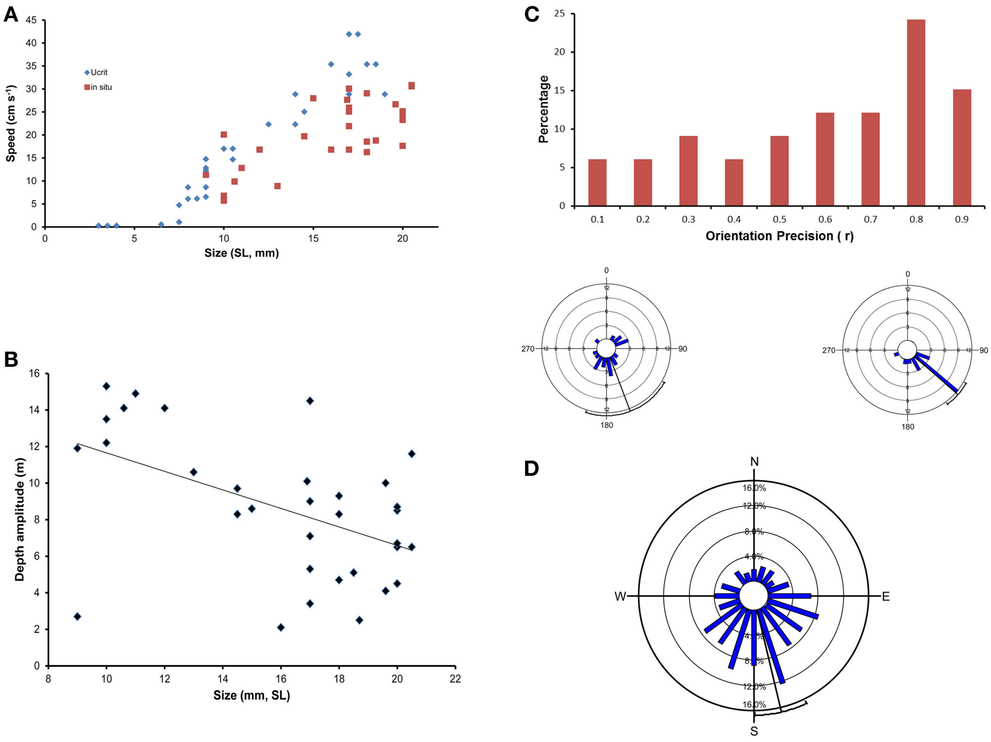

FIGURE 1 | (A) Ontogenetic change in swimming speed as measured in a laboratory raceway (critical speed [Ucrit], Diamonds), and in the ocean (*in situ* speed, Squares) of a serranid, *Epinephelus coioides*. Note the wide range in speeds at any size, particularly in the ocean. Although there is a significant increase in speed with size for both measures, the laboratory measure relationship explains 92% of the variation over the common size range whereas the *in situ* relationship explains only 54%. Data from Leis et al. (2007, 2009). **(B)** Ontogenetic change in *in situ* depth amplitude (difference between greatest and least depth) in larvae of a serranid, *Epinephelus coioides*. Note the wide range in depth amplitude at any size. The significant ontogenetic decrease in depth amplitude explains only 25% of the variation. Size of larvae is standard length (SL). Data from Leis et al. (2009). **(C)** Frequency distribution of *in situ* orientation precision (*r*, length of the mean vector) of 33 individual larvae of a serranid, *Epinephelus coioides*. The circular insets show the distribution of swimming bearings of two individuals measured every 30 s over a 10 min observation period. Although both individuals have significantly directional swimming to the South-East, the one on the left ($r = 0.43$, $p = 0.02$) has a more meandering swim path than the one on the right ($r = 0.89$, $p << 0.0001$). Data from Leis et al. (2009). The thin black radius is the mean direction, and the arc at its end is the 95% confidence interval. **(D)** *In situ* directional swimming by larvae of a pomacentrid, *Chromis atripectoralis* off the west side of Lizard Island, Great Barrier Reef, showing the frequency distribution of mean swimming bearings of 205 individually measured larvae with significant within-individual swimming directionality. The among-individual swimming direction was to the South-South-East (mean = 166.7 ± 12.8°), and highly significant ($p << 0.0001$, Rayleigh Test), but 22% of larvae swam in a direction that differed more than 90° from the mean. Data from Leis et al. (2014).

Relatively few published studies address the effects of ocean acidification on sensory systems or behaviour of fully pelagic larvae, although the numbers of such publications are increasing (Nagelkerken and Munday, 2016). Much of the experimental work on the effects of ocean acidification has been done on fish that are in transition between the pelagic dispersal stage and the relatively site-attached demersal stage. How far the young fishes are through this transition varies, as does the nomenclature used for them by researchers. A study may use settlement-stage larvae captured in light traps as they approach a reef from open water, but then held in a low-pH environment for several days (usually four) before experiments are undertaken. Or, it may use larvae reared in captivity (usually in low pH conditions) and then tested at their normal age of settlement. Larvae undergoing the major ecological transition from being a pelagic animal to being a demersal animal are also undergoing major physiological, morphological and behavioural transitions. For example, the "very high swimming speeds of pre-settlement larval reef fishes are accompanied by the highest rates of oxygen uptake found in ectothermic vertebrates, but once the larvae settle, their capacity for rapid oxygen uptake falls, and the ability for high-affinity oxygen uptake at low oxygen levels increases": they become hypoxia tolerant (Nilsson et al., 2007). Similarly, swimming abilities of larvae abruptly decrease upon settlement (Leis et al., 2011a). In fact, the transitions in physiology and morphology can begin some time before the larvae reach their settlement habitat (Holzer et al., 2017). Therefore, caution is required in assuming results based on larvae in transition apply to fully pelagic individuals. Publications on studies that hold wild settlement-stage larvae in low pH conditions for several days before testing seldom describe the tanks in which they are held. The pelagic-to-demersal transition can be slowed by holding the larvae in relatively featureless conditions (McCormick, 1999; Holzer et al., 2017). This approach means larvae undergo minimal transition to their demersal stage before testing, and if it is used, should be mentioned in methods sections of publications. Even more caution is required when assessing results based on young juveniles that have been settled for weeks or longer. Very few demersal bony fishes avoid the pelagic life history stage entirely (Leis, 1991), but the damselfish *Acanthochromis polyacanthus* is one. This species hatches on the reef well-developed at a relatively large size (Kavanagh, 2000), and is frequently used in experimental work. However, the use of *A. polyacanthus* young as proxies for pelagic larvae of other species is questionable, as is emphasized by the fact that it's recently hatched young do not undergo the transition from high oxygen consumption to hypoxia tolerance, being well-adapted to hypoxia and having relatively low maximum rates of oxygen uptake from hatching (Nilsson et al., 2007). Therefore, it is important to take into account not only the species that has been tested, but also its life-history stage.

The present evaluation is confined to marine early-life history stages of fishes. A recent paper (Ashur et al., 2017) summarizes the effects of acidification on chemosensation, hearing, and vision in aquatic invertebrates and fishes. The results of that review relevant to the present paper will be drawn upon, plus a few additional publications. Behaviours of relevance to dispersal will also be considered: swimming, lateralization, settlement timing. The early life-history nomenclature used in Ashur et al. (2017) is that of the publications they reviewed, but no standard nomenclature was used by those studies: e.g., settlement-stage larvae held in laboratory tanks for 4 days are called settlement-stage larvae or juveniles in different studies. The nomenclature used here (defined in **Table 1**) is based on examination of the methods sections of the original publications, regardless of nomenclature used therein.

Chemosensation

Adding Sundin et al. (2017) to the relevant studies listed by Ashur et al. (2017) gives nine studies of chemosensation covering eight species of two families (**Table 1**). Seven species are Damselfishes (Pomacentridae), one of which is *A. polyacanthus*, and the eighth, a Grouper (Serranidae). Three study-by-species combinations are on reared, settlement-stage larvae; four are settlement-stage larvae from light traps held in the laboratory for 4 days; and three are settled juveniles (two of which are *A. polyacanthus*, and the third, a reared Grouper). Only two are on fully pelagic larvae: reared Damselfish (*Amphiprion percula*). Eight studies detected an acidification-induced change in behaviour: either a reversal or loss of normal behaviour, or a decrease in it's prevalence. Only a study on the reaction to predator chemical cues of 3-month old *A. polyacanthus* juveniles did not detect an effect of acidification (Sundin et al., 2017). So, for chemosensation, acidification has the consistent effect of altering normal behaviour in pelagic larvae, and those in transition during settlement.

Hearing

Adding Castro et al. (2017) to the relevant hearing studies listed by Ashur et al. (2017) gives four studies covering four species of four families (**Table 1**). One species is a Damselfish, plus one each Goby (Gobiidae), Croaker (Sciaenidae), and Barramundi (Latidae). Two studies are on settlement-stage larvae, one on both presettlement and settlement-stage larvae, and one on recently settled Damselfish, all reared. In all studies, acidification caused a change in behaviour in relation to a habitat sound. So, for hearing, the results are consistent, and apply to a range of families and early life-history stages, although with only four studies, more research on hearing in fish larvae is needed.

In addition, Ashur et al. (2017) list 10 studies on the effects of acidification on otolith size or shape in marine fish early-life history stages. Six record an increase in size or change in shape, four found no change. In none of these studies was hearing investigated, even though there are theoretical reasons to expect changed otoliths will change hearing (Lychakov and Rebane, 2005). The otoliths of fishes are involved in both hearing and balance, and otolith size may be more influential on balance and swimming than on hearing (Popper et al., 2005). So it is difficult to predict how changes in otolith shape or size would influence hearing. The mixed results of the effects of acidification on otolith size and shape imply that there will be no simple answer. Therefore, no conclusion is attempted here about the sensory implications of changes in otoliths.

Vision

Ashur et al. (2017) list four relevant vision studies to which can be added Allan et al. (2014) and Munday et al. (2016). These cover six species of three families (**Table 1**): four are on Damselfish (one is *A. polyacanthus*), and one each on a Goby and Yellowtail (Carangidae). Three are on reared larvae, either early preflexion or settlement-stage (Allan et al., 2014). Two are on settlement-stage larvae from light traps held in laboratory tanks for 4 days, and one on 55–80 mm, settled *A. polyacanthus* juveniles. The last found a reduced retina maximal flicker frequency, which could impair the fish's capacity to react to fast events. Acidification caused changes in all three vision-related anti-predator behaviour studies. Newly hatched goby larvae had a change in phototactic response (Forsgren et al., 2013). Yellowtail preflexion larvae had no change in startle response or phototaxis (Munday et al., 2016).

In addition, two studies document developmental damage to the eyes of either preflexion or post-flexion reared larvae of Cod (Gadidae) and Tuna (Scombridae) (Frommel et al., 2012, 2016) (**Table 1**). This sort of damage could impair vision, with a variety of deleterious effects on the larvae. It is noteworthy that studies reporting morphological damage to organs of fish larvae do not always mention the full range of organs examined, so there may be unreported results of no acidification-related eye damage.

Although, all but one study report an effect of acidification on vision, none directly tested whether acidification would adversely effect vision in a way that could influence orientation. This might include, for example, using a celestial cue for orientation or using light intensity for adjustment of vertical distribution.

Physio-Chemical

A single study on reared post-flexion larvae of catadromous Barramundi (Latidae) reports acidification changes to temperature and salinity preferences (Pistevos et al., 2017), and also reports a change from avoidance to preference for

TABLE 1 | Studies of effects of acidification on sensory function or behaviour relevant to dispersal of marine fish larvae.

Sense or behaviour	Pomacentridae	Other families	Stage	Stage	Stage	Stage	Acidification effect	No acidification effect
	Studies/genera/species	Studies	PreL, PostL	Stl	Stl+	Stj		
Chemosensation	8**/3/7	Serranidae (1)	2	3	4	3**	11*	1*
Hearing	1/1/1	Gobiidae (1), Sciaenidae (1) Latidae (1)	1	2	1	1	5	0
Vision	4*/3/3	Gobiidae (1), Scombridae (1), Gadidae (1), Carangidae (1)	4 (2†)	1	2	1*	7* (2†)	1
Physio-chemical	0	Latidae (1)	1	0	0	0	1	0
Habitat cue	0	Latidae (1)	1	0	0	0	1	0
Swimming	1/1/1	Carangidae (2), Coryphaenidae (2), Rachycentridae (1) Sparidae (1), Sciaenidae (1), Atherinidae (1) Latidae (1)	9	2	0	0	3	7
Lateralization	3*/2/2	nil	0	0	2	1*	3	0
Settlement timing	1/1/1	nil	0	0	1	0	1	0
Total	18	18	18 (2†)	8	10	6***	30**(2†)	9*

The pomacentrid Acanthochromis polyacanthus, lacks a pelagic larval stage, so its relevance to questions of larval dispersal is arguable: the number of studies involving A. polyacanthus is indicated by asterisk (*). (†) Indicates studies showing developmental damage to the eye, not behavioural impairment of vision. Hearing category does not include studies that examined only size or shape change of otoliths. Life history Stage: PreL, Preflexion larva (before caudal-fin formation); PostL, Postflexion larva (caudal fin present, but not competent to settle); Stl, Settlement-stage; Stl+, Settlement-stage plus 4 days in laboratory; Stj, Settled juvenile.

estuarine water in preflexion larvae (**Table 1**). The latter may be a response to either physio-chemical or olfactory cues.

Swimming

Nine studies concern aspects of swimming, eight with reared larvae of various stages, and one with wild, post-flexion Silverside (Atherinidae) larvae (**Table 1**). The Damselfish and Barramundi studies involved settlement-stage larvae. Mean routine or critical swimming speed, both laboratory measures, decreased in Carangidae (Munday et al., 2016, 2017a), Coryphaenidae (Bignami et al., 2014), and Latidae (Rossi et al., 2015), but did not change in Atherinidae (Silva et al., 2016), Coryphaenidae (Pimentel et al., 2014), Pomacentridae (Munday et al., 2009a), or Rachycentridae (Bignami et al., 2013). Other aspects of swimming behaviour had no or minor changes in Gadidae (Maneja et al., 2013), Sciaenidae, and Sparidae (Pimentel et al., 2016). The measures of swimming most relevant to dispersal—*in situ* speed and endurance—were not tested. The mixed results with swimming speeds are in contrast to the much more consistent results with sensory function. There is little evidence for a widespread effect of acidification on swimming.

Lateralization

Three studies on Damselfishes tested acidification effects on lateralization. Two used wild settlement-stage *Neopomacentrus azysron* larvae from light traps held 4 days in laboratory tanks (Domenici et al., 2011; Nilsson et al., 2012), and the third used month-old juveniles of *A. polyacanthus* (Welch et al., 2014). The first two studies report a loss of lateralization, and the third a decrease in lateralization.

Settlement Timing

A single study on wild Damselfish *Pomacentrus chrysurus* settlement-stage larvae held for 4 days in the laboratory in low pH conditions found that peak settlement shifted from new to full moon (Devine et al., 2012).

Levels of Acidity Used in Published Studies

The levels of acidity used varies amongst studies. The large majority (32) of studies on senses used atmospheric CO_2 levels predicted for middle and/or end of this century (550–1020 μatm): all but two of these found detrimental changes to sensory performance. One vision and three hearing studies with lowest tested CO_2 values above end of century values (1368–1675 μatm) all found an effect. Amongst otolith-only studies, five used mid-to-end of century values, and five used more acidic conditions (1050–1800 μatm), and both low and high CO_2 groups had the same result: three studies with a change in otolith size or shape, and two with no change. For swimming, six studies used CO_2 values for the middle to the end of the century (two had an effect, four did not), whereas four used values of 1400–1800 μatm (one had an effect, three did not). In some cases, higher CO_2 levels were selected based on regional differences in ocean pH such as upwelling (e.g., Castro et al., 2017), but in others, it was not clear upon what basis more acidic conditions were chosen. However, it does not appear that acidity very much higher than expected by 2100 is required for detrimental sensory performance or behaviours to be likely. Most acidification studies use CO_2 levels for the middle to end of this century, but for some marine environments temperature may have already reached very damaging levels before this. Coral reefs, for example, are already experiencing repeated serious bleaching, and may be so degraded by mid-century (Hughes et al., 2017) that questions about acidification effects on larval-fish dispersal may be secondary to questions about whether adult habitat will be able to support reef-dependent fishes.

SUMMARY OF RELEVANT LITERATURE

Several conclusions arise from this evaluation of studies on the effects of acidification on senses and behaviours of fishes during their marine early life history. First, the effects on sensory function are much more consistent than those on behaviours such as swimming speed: sensory functionality is deleteriously impacted, either reversed, lost or decreased by acidification. In only two cases was an adverse effect on sensory function not found: chemosensation in 55–80 mm *A. polyacanthus*, and vision in preflexion Yellowtail carangid. Second, chemosensation is the most studied sense ($n = 9$), followed by vision and swimming ($n = 8$ each), and hearing ($n = 4$). Third, studies on senses—particularly chemosensation and vision—overwhelmingly used Damselfishes and larvae at the end of their pelagic dispersal stage (settlement-stage and beyond). In fact, about half of all studies are on Damselfishes, and if swimming is excluded, nearly two-thirds of studies are on Damselfishes. Only a narrow range of 12 families has been studied thus far: 7 are coastal demersal (1 catadromous), 1 coastal epipelagic, and 4 oceanic or neritic. Most studies used tropical or warm temperate species, and there is so little overlap in the studied senses or behaviours that no conclusions can be reached about whether there are latitudinal differences in acidification effects. This situation applies to the general question of whether larval-fish dispersal differs between high and low latitudes (Leis et al., 2013). No clear conclusions can be reached because of the very large differences in taxa (usually at the Order level) between low and high latitudes, and because there are relatively few studies on aspects of larval behaviour or sensory abilities relevant to dispersal from high latitudes (Leis et al., 2013). Fourth, there is little, if any, indication that life-history stage influences whether acidification will have an effect, but this has to be qualified by noting that younger, less developed larvae are understudied, except for swimming. In the context of orientation of swimming, the lack of work on preflexion larvae is less important than for post-flexion larvae, because swimming ability of preflexion larvae is much less than that of older larvae (Fisher and Leis, 2009). In contrast, larvae control their vertical distribution for nearly all of their PLD. In one of three cases young *A. polyacanthus* had results that differed from earlier life history stages of other Damselfishes, emphasising the need for caution in the use of this species as a proxy for the pelagic stages of other species. Of course, it would be preferable to have studies across a wider range of taxa, and with more emphasis on larvae before they start their transition to the demersal environment. However, the consistency of the results to date provide reason to expect that acidification will have deleterious effects on the sensory systems and some behaviours of marine fish larvae of a range of species. Regardless, we need to spread our taxonomic and ontogenetic nets wider to include more families and more presettlement-stage larvae, to obtain a firmer basis of knowledge.

IMPLICATIONS: WILL THE "BIO" IN "BIOPHYSICAL LARVAL DISPERSAL" BE LOST?

The loss or diminution of sensory function due to acidification has serious implications for the orientation ability of fish larvae in the pelagic environment, and for the ability of settlement-stage larvae to locate suitable settlement habitat. This has been mentioned before numerous times, but without much detail: e.g., Munday et al. (2009b). The studies evaluated here provide consistent evidence that orientation depending on olfaction, hearing, vision, and lateralization will be disrupted. The effect of acidification on magnetic and celestial senses has not been examined, but given the nature of the source of this sensory dysfunction (Nilsson et al., 2012; Nilsson and Lefevre, 2016), it seems likely that they, too, will be disrupted. In contrast, it does not seem that swimming itself is influenced very much, if at all, by acidification.

The single study showing a change in settlement timing is concerning, as one would expect that the relatively precise settlement timing normally found in many species has evolved to maximize arrival at settlement habitat and minimize mortality during the settlement transition. If true, then settlement at non-optimal times would result in lower recruitment.

An inherent part of the biophysical dispersal paradigm is that fish larvae influence their dispersal, but without the ability to orientate their swimming or control vertical position or to react appropriately to habitat cues, their ability to influence dispersal either directly or indirectly will be limited. In short, the larvae will disperse in a more passive manner, and the biophysical dispersal paradigm will, in theory and in fact, be lost and replaced by a passive dispersal paradigm. Modelling indicates that dispersal by passive larvae results in a smaller proportion of larvae reaching settlement habitat, a lower level of self-recruitment, and increased mean and median dispersal distances: we can expect the same for real fish larvae in a low pH ocean. This means the shape and height of dispersal kernels which have evolved in the ocean over long periods of time will be altered by human generation of atmospheric CO_2 over a few decades. In addition, the behaviours that lead to bet-hedging and locating new locations will decrease or be lost due to decrease or loss in orientation ability.

We are only now beginning to develop a clear understanding of the biophysical dispersal paradigm, and if it is overturned by ocean acidification, it is ironic that it will be replaced by the traditional passive dispersal paradigm. This may make the job of dispersal modellers simpler by eliminating the need for understanding of and integration into models, of a range of behaviours and abilities that change with ontogeny of larvae. But the cost will be high to aquatic ecosystems and the demersal fisheries from which humans derive a great deal of their protein. We don't know to what extent all of this will apply to higher latitude, cold water demersal fishes and their larvae, just as we don't know if larval dispersal in general differs with latitude (Leis et al., 2013). More research on the effects of acidification on sensory systems of larvae of high-latitude species and on non-perciform species generally, should be a priority.

Ocean acidification may also adversely effect other aspects of larval-fish biology and behaviour such as predator avoidance (Wang et al., 2017), growth rates, and feeding ability, among other things (Nagelkerken and Munday, 2016). Any of these could lead to increased mortality and reduced recruitment, but the results of studies of acidification effects on them have not been consistent. They have not been reviewed here because in an acidified ocean, these aspects would apply equally to larvae that are passively dispersed as to those that behaviourally participate in and influence their dispersal. That is, they would be expected to have a similar effect on the passive dispersal paradigm as on the biophysical dispersal paradigm.

A best-case scenario is that marine fish species may be able to acclimate or adapt through natural selection so their larvae can deal with the low-pH, high temperature conditions of the near future pelagic ocean in which larvae live, develop, grow, and disperse. The exact physiological and biochemical mechanisms involved in sensory disruption in fish larvae are not entirely understood, so prediction is difficult, but there are reasons to expect within-generation acclimation will not be possible (Nilsson and Lefevre, 2016), and research so far supports this expectation (Munday et al., 2013b, 2014).

Research on the possibility of transgenerational acclimation to elevated CO_2 has returned mixed results. Some report improved growth and survival in offspring (Miller et al., 2012; Murray et al., 2014), while others report no or limited capacity for transgenerational acclimation of olfactory responses or predator escape (Allan et al., 2014; Welch et al., 2014). This led to speculation that metabolic traits may have greater potential than behavioural traits for transgenerational acclimation to elevated CO_2 (Welch et al., 2014).

Most studies that test the effects of acidification on senses and behaviours of fish larvae show variation in sensitivity among individuals. This has led to conclusions that there is clear "potential for natural variation in sensitivity among individuals to lead to genetic adaptation in marine fishes" (Leduc et al., 2013). However, this is true only if the variation has a genetic basis and is heritable a recent study on *A. polyacanthus* has found this for temperature (Munday et al., 2017b). But, thus far, there is no evidence of this for acidification, as has been noted by several—(e.g., Munday et al., 2013a). In larval fishes, ontogenetic changes in many aspects of physiology, behaviour, and morphology are large and ongoing, and variation in sensitivity can have a number of non-genetic bases, among which are variation in size or age of larvae, in how far metamorphosis has progressed, or in nutritional or physiological condition. An example is (Munday et al., 2013a), a study cited by Leduc et al. (2013). In the publication, studied fish were sequentially called larvae upon capture and CO_2 treatment, larvae and juveniles during olfaction tests, and juveniles during observations of behaviour and mortality rates (Munday et al., 2013a): the fish were metamorphosing during the experiments, and individuals varied in developmental stage at any time. Larvae of the study species also varied in age and size at capture: 16–21 days (Munday et al., 2013a), and 15.2–18.0 mm total length (Fisher et al., 2005). These variations might contribute to variation among individuals in sensitivity to acidification at any time. Therefore, although variation among individual larvae in sensitivity to acidification may indicate heritable "raw material" upon which selection can act, other possibilities exist. As noted by Munday et al. (2013a) "quantitative genetic analyses, such as comparisons of parent-offspring or half-sib variation will be required to estimate heritability."

There are two ways of approaching the question of adaptation: measuring standing genetic variation in pH-sensitive traits, and conducting evolution experiments in real time (Sunday et al., 2014). Both approaches have advantages and disadvantages, and the latter especially apply to species such as marine fishes with relatively long life cycles and complex life histories. I was unable to find any published studies using genetic variation to study pH-sensitive traits relevant to larval dispersal in marine fishes. An approach that is used for species with short generation times such as plankton is laboratory rearing over multiple generations in high CO_2 conditions to determine if adaptation takes place (Munday et al., 2013c). This would be extremely challenging in marine demersal fishes because the conditions and challenges that larvae face in the pelagic environment while dispersing are so different than those faced by the more site-attached, bottom-associated adult. So, perhaps it is not surprising that there are apparently no published attempts to do this with marine, demersal fishes. At present, adaptation to acidification in marine fishes is an undemonstrated possibility. It is noteworthy that where adaptation has been demonstrated in marine species with very short generation times, adaptation has taken several hundred generations to occur (Sunday et al., 2014), and CO_2 levels expected before or by the end of this century will already be causing sensory dysfunction in marine fish larvae. In short, even if adaptation to elevated CO_2 levels is possible there is "considerable risk that the present rate of CO_2 increase is too high to allow adaptation through natural selection" (Regan et al., 2016). Further, the physiologist who discovered the mechanism behind elevated CO_2 sensory dysfunction in fish larvae has written: "since atmospheric CO_2 levels have probably remained below 500 μatm for the last 30 million years, there is a great risk that genes needed for coping with a sustained elevation of CO_2 are no longer functional" (Nilsson and Lefevre, 2016).

Behaviour and sensory systems of larval marine fish species may or may not acclimate or adapt to elevated (and rising) CO_2 levels, but there is little relevant research on the question, in spite of calls for it. Assuming that acclimation or adaptation will happen quickly enough to overcome the rapid rate at which CO_2 is rising is optimistic given our current level of understanding. A more certain result can be achieved by strongly reducing anthropogenic CO_2 production so ocean pH does not decrease as it will under a "business as usual" scenario.

CONCLUSIONS

Research to date consistently shows that ocean acidification will have a negative effect on the sensory abilities of larval, marine perciform fishes. This will adversely impact on the ability of the larvae to orientate in the ocean, to find settlement habitat and to adjust their vertical distribution, and thus influence their dispersal. In short, the biophysical larval dispersal paradigm will no longer apply. Acidification will also decrease the bet-hedging and colonization of new locations that behavioural variability enables. Dispersal modelling predicts that, as a result, recuitment of demersal fishes will decrease, as will local recruitment while mean and median dispersal distances will increase.

AUTHOR CONTRIBUTIONS

JL conceived, drafted, and is accountable for all aspects of this work, interpreted the data, and gave final approval for publication.

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Behavior of Brooded Coral Larvae in Response to Elevated pCO_2

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Elevated pCO_2 threatens coral reefs through impaired calcification. However, the extent to which elevated pCO_2 affects the distribution of the pelagic larvae of scleractinian corals, and how this may be interpreted in the context of ocean acidification (OA), remains unknown. We tested the hypothesis that elevated pCO_2 affects one aspect of the behavior (i.e., motility) of brooded larvae from *Pocillopora damicornis* in Okinawa (Japan), and used UV-transparent tubes that were 68-cm long (45 mm ID) to incubate larvae on a shallow fringing reef. Replicate tubes were filled with seawater at ~400 μatm or ~1,000 μatm pCO_2, stocked with 50 larvae each, and incubated vertically for 12 h with their midpoints at 0.3-m (shallow) or 3.3-m (deep) depth over a reef at 4-m depth. Larval behavior was assayed through their position in the tubes, which was scored *in situ* every 4 h beginning at 08:00 h. Lipid content was measured at the end of the experiment as a potential driver of behavior through its effects on larval buoyancy. Larval position in the tubes varied between depths and time of day at ~400 μatm pCO_2 and ~1,000 μatm pCO_2. At ~400 μatm, larvae moved toward the top (0.1-m) of shallow tubes throughout the day, but in the deep tubes they aggregated at the bottom of the tubes from 08:00 to 20:00 h. In contrast, larvae incubated at ~1,000 μatm pCO_2 aggregated at the bottom of shallow tubes at 08:00 and 20:00 h, however in the deep tubes they were found in the bottom throughout the day. As lipid content of the larvae declined 23–25% at ~1,000 vs. ~400 μatm pCO_2, loss of lipid may be a cause of modified larval behavior at high pCO_2. If the pCO_2-mediated changes in behavior and lipid content during this short experiment occur during longer exposures to high pCO_2, our results suggest OA could alter the dispersal capacity of brooded coral larvae.

Keywords: ocean acidification, corals, *Pocillopora damicornis*, brooded larvae, behavior

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INTRODUCTION

Understanding the processes contributing to the distribution of organisms is a cornerstone of ecology (Hastings and Harrison, 1994), and in the marine environment, behaviorally-modulated dispersal of pelagic larvae plays a critical role in determining the spatial distribution of benthic populations (Levin, 2006). Larval behavior contributes to the capacity for pelagic larvae to disperse, which influences gene flow and connectivity among populations (Cowen and Sponaugle, 2009). To quantify the movement of pelagic larvae in the marine environment, their vertical position in the water column must be measured with a high degree of temporal resolution (i.e., hourly), because their vertical position can change within hours (Harii et al., 2002), and vertical changes as small as

50–100 cm can provide exposure to seawater with differing velocities (Szmant and Meadows, 2006) that are likely to vary throughout the day (e.g., with the tidal cycle). High-resolution descriptions of the vertical position of larvae in the water column requires analyses of their ability to swim, their intrinsic buoyancy, and environmental conditions (e.g., seawater density, temperature, and vertical advection) that together translate into the capacity for dispersal (Metaxas, 2001; Levin, 2006; Gleason and Hofmann, 2011).

The aspects of larval behavior modulating their vertical migration through swimming and buoyancy as a function of environmental conditions and ontogeny (sensu Paris and Cowen, 2004) have been extensively studied in marine organisms (Chia et al., 1984). For coral reef organisms, behaviorally-mediated dispersal of pelagic larvae plays a strong role in determining benthic and pelagic community structure (reviewed in Jones et al., 2009), with these effects evident over areas as small as $\leq$300 m^2 (Jones et al., 2005; Almany et al., 2007) and as big as tens-to-hundreds of kilometers through connectivity mechanisms (Cowen et al., 2006). The framework-builders of coral reefs (i.e., scleractinians) are sessile as adults, but like reef fishes (Doherty et al., 1985) and many other marine benthic invertebrates (Thorson, 1950), are dependent on pelagic larvae for dispersal (Harrison and Wallace, 1990). The dispersal of pelagic larvae from undisturbed to disturbed coral reefs is a key factor mediating the recovery of coral populations that have been severely depleted in abundance (van Oppen et al., 2008). One main finding in studies on connectivity among benthic communities on coral reefs is strong spatio-temporal heterogeneity (Cowen and Sponaugle, 2009), which is an enduring feature of community ecology (Cornell and Lawton, 1992) that also emerges in long-term analyses of community structure (Edmunds, 2000; Bruno and Selig, 2007; Pratchett et al., 2011) and studies of the settlement choices of sessile invertebrate larvae (Whalan et al., 2015).

Environmentally-induced changes in the motility of pelagic larvae are likely to affect their vertical distribution in the seawater column, thereby exposing them to differing abiotic factors (e.g., vertically stratified seawater flow) that can modify the direction, distance, or speed of their dispersal. Changes in larval settlement behavior (e.g., delayed timing of peak settlement, extended settlement window) may also increase the dispersal potential of larvae based on their vertical distribution (*Platygyra sinensis*, Tay et al., 2011). In shallow coastal seawater, even a change in vertical distribution of a few decimeters can expose larvae to different seawater velocities, since seawater motion in such habitats typically is vertically stratified on a commensurate scale (Cowen and Sponaugle, 2009). For example, wind driven surface currents can cause the 5-cm thick surface layer of seawater over a shallow coral reef to move faster, and in the opposite direction, than seawater at 50–100 cm depth (Harii and Kayanne, 2003). Vertical migration and subsequent advection can subject coral larvae to different environmental conditions compared to the benthic adults (Hughes et al., 2000).

Although the pelagic larvae of many marine organisms are provisioned with maternally-derived defenses against environmental stress (Hamdoun and Epel, 2007), and therefore may be more resistant to stress than their parents (Haryanti et al., 2015), there is evidence that the larvae of at least some tropical scleractinians are more vulnerable than adults to changing environmental conditions (Putnam et al., 2010; Byrne, 2011). For pelagic coral larvae, one aspect of their biology that has not been tested for a response to high pCO_2 is their behavior in the swimming phase. While various physiological responses to high pCO_2, such as increased size (Putnam et al., 2013) or depressed metabolic rates (Rivest and Hofmann, 2014), have been observed in coral larvae, analysis of their behavior in the swimming phase has yet to be conducted to evaluate the implications of elevated pCO_2 for their dispersal.

In this study, the behavior of brooded scleractinian larvae under contrasting pCO_2 regimes (ambient and elevated) was investigated at two depths to gain insight into the possibility that their dispersal will change in future oceans characterized by higher seawater pCO_2 than present-day. Using experiments conducted on the shallow reefs of Okinawa (Japan), we tested the hypothesis that vertical movement of larvae from *Pocillopora damicornis* is affected by high pCO_2 ($\sim$1,000 μatm). *P. damicornis* was chosen since it is a brooding scleractinian coral that releases planula larvae on a monthly lunar cycle. Larvae were incubated in acrylic tubes filled with seawater at either ambient or high pCO_2, and suspended vertically in the seawater above a fringing reef. First, the vertical position of the larvae in the tubes was scored over 12 h to test their response to a contrast of ambient vs. elevated pCO_2 in shallow water. The experiment was repeated with the tubes incubated in deeper water, and combination of the two experiments provided an orthogonal contrast of the effects of pCO_2 and depth on larval behavior. Second, the hypothesis that the total lipid content of the larvae would change under elevated pCO_2 vs. ambient pCO_2 was tested to explore the possibility that lipid metabolism mediated the vertical position of the larvae in seawater. Lipids play a role in the buoyancy regulation of a wide variety of planktonic marine organisms (Campbell and Dower, 2003), so we reasoned that modulation of lipid content in larvae from *P. damicornis* could modify their vertical position in the water column by buoyancy effects (Harii et al., 2002).

MATERIALS AND METHODS

Twelve colonies of *Pocillopora damicornis* (Linnaeus 1758) were collected in July and August 2016 from $\sim$1-m depth on a patch reef on the northwest shore of Okinawa (26°40′18.24′′ N, 127°53′4.78′′ E). Colonies were collected prior to expected larval release in Okinawa in both months (S. Harii, unpublished data on the study site), in which peak release occurred $\sim$7 days after the new moon. At the times of collection, the ambient seawater temperature at the study site was $\sim$29°C.

Following collection, colonies were transferred to Sesoko Station, part of the Tropical Biosphere Research Center University of the Ryukyus, where they were incubated outdoors in individual containers exposed to natural irradiance in flow-through seawater. Ambient seawater was pumped at 3.0 L min^{-1} (AC Flowmeter, Tokyo Keiso Co., Japan) from 4 to 5-m depth and stored in two 10-L reservoirs. Air was bubbled constantly in to the reservoirs at 3.0 L min^{-1} to maintain ambient seawater pCO_2 (i.e., the control conditions). Ambient seawater temperature was measured hourly at 1–2-m depth near the collection site prior to, and during, the experiment (HOBO Pro v2, Onset Computer Corporation, USA), and was 29.9 ± 0.2°C (mean ± SE, $n = 45$ days), with a daily minimum of 28.3°C and daily maximum of 31.8°C (R. Prasetia and S. Harii, unpublished data) that reflects summertime diurnal warming in this location (Takahashi and Kurihara, 2013). Temperature in the containers holding the corals was maintained within this range during the experiment (29.8 ± < 0.2°C, mean ± SE, $n = 31$) using a chiller (ZR-130E, Zensui, Japan).

Planulae released from *P. damicornis* during the first quarter moon of July and August were collected at ∼05:00 h following their release at ∼03:00 h (Isomura and Nishihira, 2001), using containers lined with 110 μm plankton mesh. Larval color and approximate size were evaluated by eye. As larvae from *P. damicornis* are physiologically dissimilar among days of release (Fan et al., 2002; Cumbo et al., 2013), larvae were collected from the inferred day of peak release and pooled among colonies releasing larvae on this day. Larvae from July and August were used to test the effects of pCO_2 (two levels) and depths (two levels) on larval behavior, and the experiment was conducted in two parts. The first part (July 2016) tested the effects of two pCO_2 regimes on larval behavior with the tubes positioned with their upper opening adjacent to the air-water interface of the seawater (hereafter "shallow" tubes), and the second part (August 2016) tested the effects of the same two pCO_2 regimes on larval behavior with the tubes positioned with their upper opening ∼3–4 m below the surface (hereafter "deep" tubes).

Response of Larval Behavior to High pCO_2

To determine the position of *P. damicornis* larvae in the seawater in response to high pCO_2, larvae were transferred from collection containers to UV-transparent acrylic tubes (UV-T, ACRYLITE Colorless 0070 GT, Evonik Industries, New Jersey, USA) and incubated *in situ* at two depths, which centered the tubes vertically at ∼0.3 m (July 2016) or ∼3.3 m (August 2016). The tubes had a wall thickness of 6 mm, were 68-cm long with an inner diameter of 4.5 cm, and were sealed at either end with UV-T acrylic caps. A 6-mm hole was drilled in the top cap so the tubes could be filled with seawater; the hole was later covered with vinyl electrical tape. While the objective was to completely fill the tubes with seawater, in most cases small bubbles were introduced during the filling process and combined when the tubes were positioned vertically to create an air gap of ≤1-cm height at the top of the tube. The acrylic in these tubes transmitted ∼92% of ultraviolet radiation (UV-R) (280–400 nm) (J. Bergman, unpublished data), ensuring larvae were exposed to ecologically relevant light conditions for shallow seawater (Gleason and Hofmann, 2011). Previous studies of the vertical movement of *P. damicornis* larvae in acrylic tubes (Harii et al., 2002), as well as preliminary observations of larval behavior used in the present study, show that larvae of *P. damicornis* exposed to ambient seawater generally aggregate either in the top or bottom 0–2 cm of tubes regardless of light conditions (i.e., light vs. dark). Therefore, the vertically-oriented tubes were marked into two sections for the purpose of scoring the larvae by position: an upper section (21-cm length) and lower section (47-cm length), since we reasoned it would be unlikely that the larvae would accumulate in the center of the tubes. Of the larvae found in the lower section, 83–88% were located in the bottom 23 cm of the tube, which suggested that the greater size of the lower scoring section in the tubes did not upwardly bias estimates of larvae scored as moving downward.

Eight tubes were used for each experiment, during which four were filled with ambient (∼400 μatm pCO_2) seawater, and four with treatment (∼1,000 μatm pCO_2) seawater that simulated the elevated pCO_2 conditions predicted to occur by 2100 under a pessimistic scenario of human activity [RCP6.0 (Moss et al., 2010; Intergovernmental Panel on Climate Change, 2014)]. Once tubes were filled with seawater, 50 larvae were haphazardly selected from the larval stock obtained by pooling larvae released that morning from maternal colonies, and added using a Pasteur pipette through the 6-mm hole in the cap of the tube. The hole was sealed when the tubes were stocked with larvae. Each tube was carefully inverted to gently mix the 50 larvae, so each trial began with the larvae scattered along the length of the tube. Although the pelagic larval duration (PLD) of *P. damicornis* can be >100 d (Richmond, 1987), their larvae commonly settle ≤24 h following release (Richmond, 1987; Isomura and Nishihira, 2001; Harii et al., 2002; but see Cumbo et al., 2012), and therefore, the present incubations were designed to last 12 h starting at 08:00 h.

After the tubes were stocked with larvae on the shore, they were transported by a snorkeler to an adjacent fringing reef and suspended vertically, with the midpoint of the tubes at a median depth (MD) of either ∼0.3 m (July) or 3.3 m (August) (hereafter referred to as 0.3 and 3.3-m MD) (**Figure 1**). The median depth was recorded at the middle of the vertically oriented tubes, thus the depth range for the 0.3 m MD tubes extended from the surface to 0.7 m, and from 3 to 3.7 m for the 3.3 m MD tubes. To maintain this configuration, the tubes were attached

FIGURE 1 | Photograph of 68-cm long tubes deployed *in situ* at ∼3.3-m MD on the shallow fringing reef near Sesoko Station in August 2016. Ambient and high pCO_2 treatments were haphazardly distributed among 8 tubes.

to a weight at 5-m depth, and a float was used to keep them suspended vertically. While it is not possible to exclude an effect of time (July vs. August) in confounding the contrast of depth, experimental conditions were kept virtually identical between months to reduce temporal bias. Tubes were stocked with larvae shortly after sunrise, and were installed on the reef within 30 min of filling at ∼07:30 h. Thereafter, the vertical position of the larvae was scored every 4 h starting at 08:00 h (initial) and finishing at ∼19:30–20:00 h (sunset); the tubes were removed from the water at 08:00 h the following day and the larvae processed for lipid content (described below). At each census, the position of the larvae in the tubes was scored as the number of larvae in either the top or bottom sections of the tube. Tubes were not evaluated at night because of logistical constraints associated with nighttime snorkeling. The percentage of the total number of larvae present in the tubes at the time of each sampling was calculated for the top section of the tubes and used as the response variable to evaluate the effects of the treatments (depth and pCO_2).

Carbonate Chemistry

High pCO_2 seawater was prepared in a single 10 L plastic reservoir by bubbling air or pure CO_2 gas into seawater using a mass-flow controller (HORIBASTEC, SEC-E40, Japan) that supplied gas at 16 mL min^{-1}. Adjustments of ± 0.1 mL min^{-1} in the flow rate of CO_2 gas were made manually as necessary each morning leading up to the experiment to maintain the desired pCO_2, as evaluated from daily measurements of seawater pH and total alkalinity (A_T) used to calculate seawater pCO_2 using CO2SYS software (Lewis and Wallace, 1998). Seawater pH and temperature in the reservoir were measured daily between 09:00 and 11:00 h using a handheld meter (Multi 3410, WTW, Germany) fitted with a combination probe that recorded pH (±0.001 pH unit) and temperature (±0.1°C) (SenTix 940, WTW, Germany). The probe was calibrated daily prior to use with three NBS buffers (Nacalai Tesque, Japan). The salinity of the seawater used to fill the larval incubation tubes was measured using a conductivity meter (TetraCon 325, WTW, Germany), and A_T was determined using open-cell titrations conducted with an autoburette titrator (Kimoto, ATT-05, Japan). Titrations of certified reference materials (batch 155) provided by A.G. Dickson (Scripps Institute of Oceanography) yielded A_T values that differed on average $\leq 1.3\ \mu mol\ kg^{-1}$ from the certified value ($SE = 9.2\ \mu mol\ kg^{-1}$, $n = 6$). Seawater pCO_2, HCO_3^-, CO_3^{2-}, and Ω_{arag} were calculated from pH, temperature, A_T, and salinity using CO2SYS (Lewis and Wallace, 1998) with dissociation constants K1 and K2 from Mehrbach et al. (1973).

Lipid Content

To test for changes in total lipid content in the larvae following incubations under ambient and high pCO_2, the initial lipid content of larvae was determined in three samples of 50 larvae, freshly released from the maternal colonies at 06:00 h and pooled among them. Each batch of larvae was placed in 1.5-mL vials for processing. The final lipid content of the larvae (i.e., 24 h after the start of incubations) was determined by processing batches of larvae in the same way following 24 h in ambient or high pCO_2 in either shallow (July) or deep (August) locations. Tubes incubated on the reef were returned to the lab 24 h after the start of each experiment (i.e., 08:00 h the following day), and all living larvae were collected by rinsing the contents of each tube into a collection container. Retrieved larvae were counted, and a single batch of 50 larvae from each tube at both depths was placed in a 1.5 mL vial for measurement of lipid content.

After transferring the batches of larvae to 1.5-mL vials, excess seawater was removed from the vials using a Pasteur pipette, and the larvae were frozen at −80°C for lipid analysis within 2–4 weeks. Following the protocol of Harii et al. (2010), modified by lengthening the extraction time in an ultrasonic bath to 15 min, lipids were extracted with 5 mL dichloromethane-methanol (6:4) at room temperature. Each batch of 50 larvae was extracted three times, with the solvent and eluted lipid pooled among extracts. Extracted lipids were concentrated in a rotary evaporator for 15–20 min, the residue was dissolved in dichloromethane 6 times, and then centrifuged to separate lipids from any remaining water. The solvent containing dissolved lipids was transferred to a new 50 mL flask after each separation. After the replicate dissolutions in dichloromethane, the samples were partially evaporated once again for ∼5 min, and passed through a ∼1 cm column of Na_2SO_4 crystals and plastic wool to remove any remaining water. Samples drained by gravity from the column into 4-mL pre-combusted glass vials (400°C for 4 h), in which they were then dried under nitrogen gas and weighed using a microbalance (±1 μg, MT5, Mettler-Toledo, USA). All solvents used were American Chemical Society (ACS) Guaranteed Reagent (GR) grade. Larval lipid content was expressed as $\mu g\ larva^{-1}$. The extraction efficiency of lipids was evaluated by comparing the lipid content of control larvae with the known lipid content of *P. damicornis* (Rivest and Hofmann, 2015).

Statistical Analysis

Statistical analyses were conducted using SYSTAT Version 11 software (Systat Software, San Jose, CA). A two-factor Repeated Measures (RM) ANOVA was used to compare the effects of depth and pCO_2 on larval position in the tubes, with time of day as the RM factor, and arcsine-transformed values of the percentage of larvae found in the top of each tube as the dependent variable. *Post-hoc* analyses were conducted as paired *t*-tests for tubes at each depth and treatment combination, testing for differences between sequential time points using an $\alpha = 0.05/3$ for three contrasts within each group. Differences in lipid content of larvae were evaluated using a two-sample *t*-test to compare the effect of pCO_2 on total lipid between depths, and a Kruskal-Wallis non-parametric test (due to violations of normality in the data) to compare lipid content after pCO_2 incubations regardless of month. Assumptions of normality and homogeneity of variance for the RM-ANOVA were assessed through graphical analyses of the residuals.

RESULTS

Four hundred larvae were used in July and August for incubations in the eight tubes. Larvae were pale brown and prolate spheroid in shape, actively swam throughout incubations, and behaved similarly to each other following release from maternal colonies in July and August (i.e., before each test of the effect of depth). Larvae used at both depths were collected on lunar day 7, which corresponded to July 10th for 0.3-m MD, and August 8th for 3.3-m MD. Seawater temperature in the 14 days prior to larval release did not statistically differ (2-sample *t*-test, $t = 0.617$, $df = 26$, $p = 0.118$) with a grand mean (pooled among those 14 days in each month) of 29.1 ± 0.1°C (±SE, $n = 28$ days) (S. Harii, unpublished data).

Behavior of Larvae in High pCO$_2$

The pCO$_2$ in the tubes did not differ between the start and end of the 24 h incubations at both 0.3-m MD ($t = 2.550$, $df = 5$, $p = 0.238$) and 3.3-m MD ($t = 0.007$, $df = 6$, $p = 0.995$) (**Table 1**). Pooling pCO$_2$ treatment levels between depths, and including both initial and final (24 h later) measurements of seawater chemistry, mean treatment levels were 1,060 ± 31 µatm pCO$_2$ and 356 ± 13 µatm pCO$_2$ ($n = 15$, ± SE). Larvae incubated in high pCO$_2$ retained their shape and pale brown color at both depths, and visually were indistinguishable from larvae incubated under control conditions. One treatment incubation tube at 0.3-m MD broke prior to the larval census at 16:00 h, and exclusion of this tube from the statistical analysis provided too few observations to test all interactions in the model. To address this limitation, observations on larval distribution at 16:00 and 20:00 h for the damaged tube were replaced with an imputed mean value calculated from the remaining 3 tubes in the same treatment group, and the degrees of freedom were reduced by one for each replacement (Quinn and Keough, 2002; Zar, 2010).

The percentage of larvae found in the top section of each tube differed between pCO$_2$ treatments in a pattern that varied among times and depths [i.e., there was a significant interaction among depth, time, and treatment, $F_{(3,\,34)} = 3.762$, $p = 0.019$, **Table 2**] (**Figure 2**). *Post-hoc* analyses were equivocal because of the small sample sizes, but sequential contrasts of times (three comparisons) suggest the interactive effect was caused by differences between 16:00 vs. 20:00 h in the high pCO$_2$ tubes at 0.3-m MD and ambient pCO$_2$ tubes at 3.3-m MD, between 08:00 vs. 12:00 h in the ambient pCO$_2$ tubes at 0.3-m MD, and between 08:00 vs. 12:00 h and 12:00 vs. 16:00 h in the treatment tubes at 3.3-m MD (all $p < 0.05$). At 0.3-m MD, the percentage of larvae in the top of the tubes in high pCO$_2$ described an inverse parabola as a function of time, increasing from ∼42 to 64% between 8:00 and 16:00 h, but decreasing to 49% at 20:00 h ($n = 43$–50 larvae tube^{-1}). Larval behavior in high pCO$_2$ contrasted with that observed at ambient pCO$_2$, where at 0.3-m MD the percentage of larvae in the upper section of the tubes increased throughout the day, starting at 28% at 08:00 h and ending at 84% at 20:00 h. At 3.3-m MD in high pCO$_2$, 25–50% of the larvae were in the upper section of the tubes regardless of time. Larval behavior was similar at high and ambient pCO$_2$ at 3.3-m MD, where in ambient pCO$_2$ the percentage of larvae in the upper section of the tubes was 28 ± 4% between 8:00 and 20:00 h (mean ± SE, $n = 16$ based on 200 larvae at each time), although it decreased to 18% ($n = 200$ larvae) at 16:00 h. Overall, 66 ± 6% and 37 ± 4% of the larvae were found in the upper section of the tubes at 0.3-m MD and 3.3-m MD in high pCO$_2$, respectively (mean ± SE, $n = 16$), and in all cases the remaining larvae were swimming and behaving normally in the bottom sections of the tubes after 12 h.

Lipid Content

The larvae used for lipid analysis were similar to one another in color and size (∼1-mm long), and were visible *in situ* when freshly released from the maternal colonies, and following 24 h in the acrylic tubes. The analytical procedure for the lipid analyses required a minimum of 50 larvae for each determination, and this restriction excluded one tube from each pCO$_2$ treatment (high and ambient) in both July and August, when 10–15% of the larvae settled on the walls of the tube after 24 h. Mean dry lipid content at 0.3-m MD was 12.19 ± 0.23 µg lipid larvae^{-1} after 24 h in ambient pCO$_2$, but this declined ∼23% to 9.38 ± 0.79 µg lipid larvae^{-1} after 24 h in elevated pCO$_2$ (both ± SE, $n = 3$). Similarly, at 3.3-m MD, mean dry lipid content was 11.96 ± 0.69 µg lipid larvae^{-1} after 24 h in ambient pCO$_2$, declining ∼25% to 8.99 ± 1.24 µg lipid larvae^{-1} after 24 h in elevated pCO$_2$ (both ± SE, $n = 3$). Lipid content of freshly released larvae did not differ between July and August ($t = 0.092$, $df = 4$, $p = 0.928$), and averaged 11.98 ± 0.27 µg larvae^{-1} (± SE, $n = 6$). As lipid content did not differ between months for larvae incubated in ambient pCO$_2$ ($t = 0.248$, $df = 3$, $p = 0.820$) or high pCO$_2$ ($t =$

TABLE 1 | Mean carbonate chemistry parameters (mean ± SE, $n = 3$–4) in sealed vertical tubes in Okinawa, initially and after a 24 h incubation in ambient or high pCO$_2$, for trials at 0.3-m MD and 3.3-m MD.

Depth	Time	Treatment	pH	pCO$_2$ (µatm)	A_T (µmol kg^{-1})	Ω_{arag}	Salinity
0.3	Initial	Ambient	8.196 ± 0.031	380 ± 35	2,232 ± 1	5.86 ± 0.28	34.6
		High	7.785 ± 0.015	1,178 ± 49	2,253 ± 1	2.73 ± 0.05	34.6
	Final	Ambient	8.197 ± 0.022	376.81 ± 24	2,232 ± 1	5.65 ± 0.19	34.5
		High	7.829 ± 0.002	1,034 ± 6	2,253 ± 1	2.78 ± 0.02	34.5
3.3	Initial	Ambient	8.227 ± 0.019	349 ± 18	2,254 ± 1	5.93 ± 0.27	34.5
		High	7.836 ± 0.013	1,018 ± 29	2,256 ± 1	2.87 ± 0.13	34.5
	Final	Ambient	8.254 ± 0.007	320 ± 7	2,254 ± 1	5.85 ± 0.08	34.5
		High	7.818 ± 0.021	1,049 ± 55	2,256 ± 1	2.57 ± 0.13	34.5

Table displays pH, partial pressure of CO$_2$ (pCO$_2$), total alkalinity (TA), aragonite saturation state (Ω_{arag}), and salinity. Treatment (pCO$_2$) conditions did not differ between initial and final measurements for all treatment in shallow ($t = 2.550$, $df = 5$, $p = 0.238$) or deep ($t = 0.007$, $df = 6$, $p = 0.995$) deployments. SE for salinity was <0.1.

TABLE 2 | Results of a two-factor RM ANOVA.

Source of variation	*df*	MS	*F*	*p*
BETWEEN SUBJECTS				
pCO$_2$	1	0.003	0.080	0.782
Depth	1	1.500	38.252	<0.001
pCO$_2$ × depth	1	0.235	6.003	0.031
Error	12	0.039		
WITHIN SUBJECTS				
Time	3	0.207	9.808	<0.001
Time × pCO$_2$	3	0.045	2.115	0.115
Time × depth	3	0.174	8.214	<0.001
Time × depth × pCO$_2$	3	0.080	3.762	**0.019**
Error	34	0.021		

Time, pCO$_2$, and depth were treated as fixed factors, and arcsine-transformed values of the percentage of larvae found in the top of each tube as the dependent variable. Interactions that were interpreted in the context of the study are shown in bold.

0.267, $df = 3, p = 0.803$), the results of the lipid analyses following incubations were pooled between months and depths to test for an overall effect of high pCO$_2$. Lipid content of the larvae differed in high pCO$_2$ from ambient pCO$_2$ and initial release (Kruskal Wallis test, $H = 9.710$, $n_1 = n_2 = n_3 = 6$, $p = 0.008$) (**Figure 3**).

DISCUSSION

In this study, the vertical position in the water column of *Pocillopora damicornis* larvae was measured as a function of pCO$_2$, depth, and time of day to test the hypothesis that their vertical positioning was affected by high pCO$_2$. Under current ambient pCO$_2$ conditions directly below the surface, freshly released larvae moved upward in vertically-oriented tubes over 12 h. Upward movement was attenuated by a 3-m increase in median depth, where ∼38% fewer larvae remained in the upper section of the tubes all day. Larval behavior in tubes close to the surface changed with exposure to high pCO$_2$, with accentuation of daytime movement that enhanced the occurrence of larvae in the upper portion of the tubes around noon, but this trend reversed in the morning and evening to favor occurrence in the lower portion of the tubes. The pattern of upwards movement at midday disappeared in tubes containing high pCO$_2$ seawater at 3.3-m MD, in which 50–75% of the larvae were found throughout the day in the bottom portion of the tubes (i.e., there was no vertical migration over the 12 h observation period). Lipid content of the larvae declined 23–25% after 24 h at high pCO$_2$ (but not ambient pCO$_2$), and changes in buoyancy due to reduction in lipid content may, therefore, have played a role in the shift in larval behavior at high pCO$_2$. Shifts in vertical position of the larvae on a scale of decimeters as a function of pCO$_2$ can cause differential advection through exposure to dissimilar current velocities (Bingham and Young, 1991) that occur on vertical scales as small as 50–100 cm in shallow seawater over coral reefs (Harii and Kayanne, 2003; Hench et al., 2008). Exposure to different flow speeds, directions, and water types can cause local retention or decreasing pelagic larval duration (PLD) (Largier, 2003; Cowen and Sponaugle, 2009), and therefore affect dispersal (Savina et al., 2010).

The vertical position of pelagic larvae in the water column allows stratified water masses moving at different speeds or varying directions to be "sampled" as larvae move up and down in the water (Largier, 2003). In Okinawa, for example, pelagic larvae are exposed to hydrodynamic features differing in flow direction and speed between wind-driven surface currents (8 cm s^{-1} north) and net seawater flow 0.5–1 m below the surface (1.5 cm s^{-1} southeast) (Harii and Kayanne, 2003), thus modifying their dispersal depending on the vertical position. For larvae in the present study, stratification of currents could lead to increased dispersal, notably for those larvae inferred to spend time in the upper 21 cm of the water column, vs. those positioned deeper in the water column (i.e., the lower 47 cm of the present tubes). Larval dispersal mediated by vertical migration through stratified seawater motion is likely to be common for coral larvae, because seawater is commonly stratified by contrasting horizontal flows speeds in reef habitats (e.g., shallow coastal waters, or on a reef crest). For instance, using a vertical resolution of 1 m, Salas-Monreal et al. (2009) demonstrated differences in east-west and north-south velocity components of seawater in the Gulf of Mexico, with these differences establishing a depth-dependent flow gradient extending from 4 to 16 cm s^{-1} between the surface and 2-m depth. Likewise, measurements of seawater velocity just behind the reef crest in Moorea, French Polynesia, revealed differences of ∼5–10 cm s^{-1} between the surface of the reef at 2-m depth, and the surface of the seawater flowing over the reef (Hench et al., 2008).

Additionally, based on the data presented here, the present study suggests that elevated pCO$_2$ will lead to a higher proportion of larvae at or near the surface of the seawater. In the few coral reef habitats where seawater pCO$_2$ is naturally elevated and localized, such as the Galápagos (Manzello, 2010), the response reported here of coral larvae to elevated pCO$_2$ may have beneficial effects. Such effects could result in dispersal away from areas of higher pCO$_2$, via surface currents that are typically of a greater magnitude than subsurface currents (Harii and Kayanne, 2003). However, the dispersal of coral larvae away from areas of high pCO$_2$ may not be advantageous in the context of OA, which is predicted to result in elevated seawater pCO$_2$ across large spatial scales so that enhanced advection of larvae would not move them to areas of reduced pCO$_2$.

The large number of *P. damicornis* larvae (an average of 55% pooled across all treatments and times of day) found in the bottom of the present tubes therefore is also likely to have ecological relevance in determining the "sampling" by larvae of multiple strata of seawater differing in seawater velocities. Larvae aggregating near the bottom of the present tubes probably would have reached the benthos ∼5 m below if they were not contained in capped tubes, and this would have accentuated the sampling of benthic substrata and possibly hastened settlement, effectively reducing PLD (Miller and Mundy, 2003). Testing of this possibility would require two changes to the present experiment: first, to provide larvae with access to a longer vertical section of seawater, and second, to census their vertical position over more than 12 h to evaluate diel periodicity in

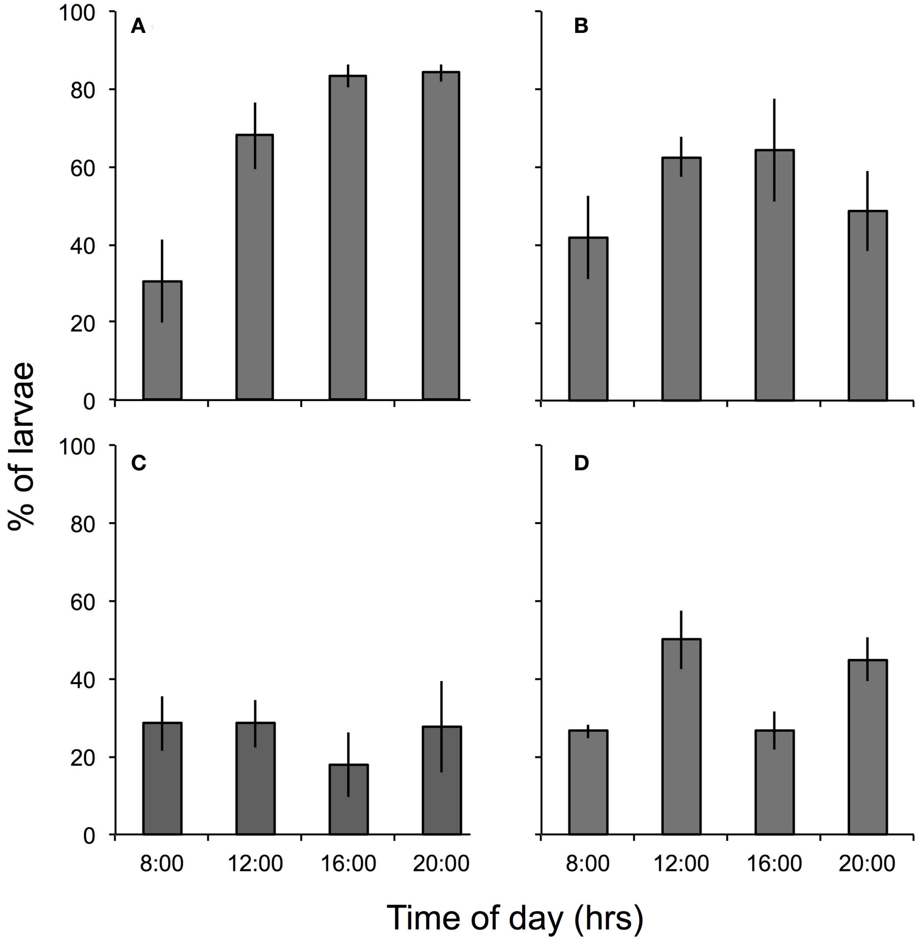

FIGURE 2 | Percent (mean ± SE, *n* = 4) of *P. damicornis* larvae in the top (0–21 cm) of tubes filled with seawater at: **(A)** ambient (~400 µatm) pCO_2, 0.3-m MD, **(B)** high (~1,000 µatm) pCO_2, 0.3-m MD, **(C)** ambient pCO_2, 3.3-m MD, and **(D)** high pCO_2, 3.3-m MD. Larval position was scored every 4 h in the first 12 h following initiation of treatment conditions at 08:00 h.

vertical movement (Hodgson, 1985). The potential implications of reduced PLD in coral larvae by accentuated downward migration at ≥1,000 µatm pCO_2 has ecological relevance, because shorter PLDs are associated with limited dispersal potential and enhanced possibilities of settlement at the natal site (Levin, 2006; Treml et al., 2012).

Lipid Content in High pCO_2

The second goal of the present study was to test the hypothesis that high pCO_2 affected the lipid content of *P. damicornis* larvae after 24 h exposure to high pCO_2 *in situ*. Exploration of this goal was motivated by the inference that a change in lipid content in response to high pCO_2 would affect larval buoyancy (sensu Harii et al., 2007). A leading determinant of buoyancy in invertebrate larvae is lipid content (Chia et al., 1984), and variation in lipid content can modulate their buoyancy, as in larvae of the abalone *Haliotis* spp. (Moran and Manahan, 2003) and a diversity of zooplankton (Lee et al., 2006). It is commonly accepted that brooded coral larvae are positively buoyant immediately following release (Oliver and Willis, 1987; Wood et al., 2016), and therefore quickly ascend to the surface of the seawater (Harii et al., 2002), where they are subject to rapid advection in wind-driven surface currents (Wolanski and Kingsford, 2014).

In the present study, the lipid content of *P. damicornis* larvae was measured at the start of the incubations and 24 h later. We infer that changes in lipid content occurred linearly over this period, which is consistent with trends observed in the larvae of other corals (Figueiredo et al., 2012) and invertebrates [e.g., abalone (Moran and Manahan, 2003) and sea urchins Sewell, 2005]. A linear decline in the lipid content of coral larvae could be a result of several non-exclusive mechanisms, including the catabolism of fatty acids through aerobic respiration (Harii et al., 2010), the incorporation of lipids into membrane phospholipids (Lee et al., 2006), or the loss of lipids in fat-rich mucus secretions (Gaither and Rowan, 2010; Ricardo et al., 2016). Distinguishing among these possibilities will require physiological analyses of different mechanisms by which lipid reserves are depleted by catabolism, and resolution of the lipids to their component classes (e.g., triacylglycerols and wax esters). The decline in lipid content of *P. damicornis* larvae that we recorded was detected

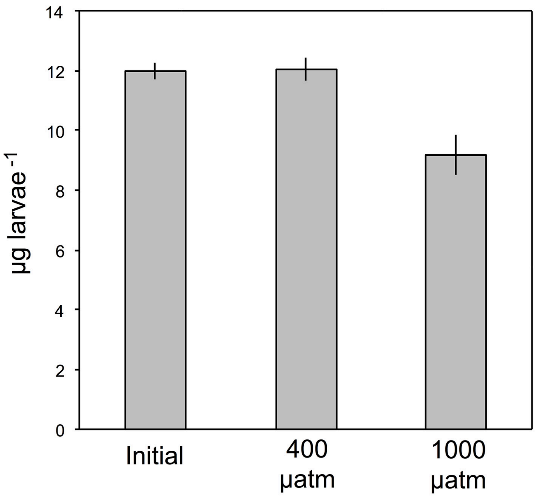

FIGURE 3 | Lipid content of *P. damicornis* larvae (μg $larvae^{-1}$) following release from the maternal colony and after 24-h exposures to ambient and high pCO_2, pooled between 0.3-m MD and 3.3-m MD (mean ± SE, $n = 6$).

based on initial and final sampling after 24 h in the treatment. Intermediate sampling that might have more completely resolved the rate of lipid decline was precluded by the challenges of working offshore at night. Nevertheless, the results show that larval lipid content declined after exposure to high pCO_2, but not after exposure to ambient pCO_2.

To our knowledge, the buoyancy of brooded coral larvae has been measured in only one study (Szmant and Meadows, 2006), likely because of the technical difficulty of separating buoyancy from swimming as mechanisms mediating larval motility in this taxon. These difficulties arise from the small size of most coral larvae, the difficulties of quantitatively sampling them in the plankton, and the challenges of quantifying the effects of ciliary swimming. However, larvae freshly released from *P. damicornis* in Mo'orea, French Polynesia, sank when they were anesthetized with eugenol, thus suggesting they were negatively buoyant (L. Bramanti, personal communication to JB), as has been described for the aposymbiotic larvae of the gorgonian *Corallium rubrum* (Martínez-Quintana et al., 2014). When interpreting larval movement in the present experiment, we therefore assume that larvae of *P. damicornis* are negatively buoyant.

Most brooded larvae of tropical scleractinians contain endosymbiotic *Symbiodinium,* which typically are vertically transmitted from the parent colony (Harrison and Wallace, 1990), and can translocate as much as 27% of their fixed carbon to the cnidarian tissue of the planula (Richmond, 1982). However, in addition to obtaining energy resources from their *Symbiodinium*, it is likely that brooded coral larvae also metabolize maternally-derived lipids to meet their energy needs (Harii et al., 2010). The use of lipid reserves for this purpose could be particularly important when the photosynthetic capacity of larval *Symbiodinium* is impaired by light or thermal stress (Haryanti et al., 2015), or in the context of our findings, by increased pCO_2, as has been seen in adult corals (Anthony et al., 2008). Understanding of the mechanisms of lipid catabolism is likely to be enhanced by more information on the lipid classes involved in the inferred catabolism. The lipids in *P. damicornis* larvae are composed of wax esters, triglycerides, and phospholipids, and as wax esters are typically the most abundant class (Harii et al., 2007; Figueiredo et al., 2012), it is reasonable to infer that lipids in the present larvae were also composed of mainly wax esters. The concentration of wax esters in the larvae of *P. damicornis* is particularly important to understanding their behavior, because wax esters have a lower density than triglycerides and phospholipids (Gurr et al., 2002; Lee et al., 2006). Wax esters are also positively buoyant in seawater (Arai et al., 1993), so they could modulate the buoyancy of larvae in which they occur.

Evidence for lipid catabolism as a mechanism to reduce the wax ester content of coral larvae comes from *P. damicornis* at Heron Island, Australia, where ≥85% of larval metabolic demand was derived from lipids under low light (∼100 μmol m^{-2} s^{-1}) conditions after 31 days in culture (Harii et al., 2010). Calculations corroborate this finding, because a larval respiration rate in *P. damicornis* of 0.15 nmol O_2 $larvae^{-1}$ min^{-1} (Cumbo et al., 2013) would consume 2.42 μg lipid $larvae^{-1}$ $day^{-1,}$ assuming lipid was the respiratory substrate and that it required 2 mL O_2 mg^{-1} to be consumed in aerobic respiration (Schmidt-Nielsen, 1997). Over 24 h in the present experiment, larvae consumed ∼2.8 μg lipid $larvae^{-1}$ in high pCO_2, so while the composition of lipids in *P. damicornis* larvae was not measured in the present analysis, it is feasible that the decline in lipid content included effects caused by catabolism of wax esters. A reduction of wax esters might be sufficient to reduce the buoyancy of the present larvae incubated at high pCO_2 and 0.3-m MD, therefore favoring downward movement in the tubes.

Elucidating the causes of the vertical movement recorded in the present analysis is challenging due to the likelihood that movement was caused by a combination of buoyancy and ciliary swimming. The inability to distinguish larval movement attributed to ciliary swimming from that attributed to passive buoyancy suggests that at least a portion of the movement recorded in the present study was a result of swimming. Utilization of ciliary swimming might explain the interactive effect of pCO_2 and depth on the position of larvae within the tubes, because the constancy of lipid content between depths at high pCO_2 suggests that changes in buoyancy were independent of depth in high pCO_2. According to this hypothesis, larvae might have swum more actively in high pCO_2. The downwards shift in vertical position of *P. damicornis* larvae in 3.3-m MD tubes (vs. 0.3-m MD) at high pCO_2 may reflect active swimming, as has been recorded for the larvae of many coral species (Vermeij et al., 2010; Martínez-Quintana et al., 2014), including *P. damicornis* (Te, 1992; Kuffner and Paul, 2004).

CONCLUSIONS

While the present study shows an effect of high pCO_2 on vertical position of the pelagic larvae of a brooding coral, this outcome should be interpreted within the constraints of the experimental design employed. First, larval behavior in acrylic tubes is likely to be constrained by the physical conditions in the tubes that differ from the open reef, notably in terms of flow regimes and wall effects. While the implications of these effects should not be ignored, the behavior of brooded coral larvae is similar in vertically-oriented tubes varying in size from 30 cm long × 1 cm ID (Raimondi and Morse, 2000) to 2.2 m long × 5 cm ID (Tay et al., 2011). This observation suggests that wall effects and tube dimensions do not alter larval behavior. Second, our interpretation of depth effects was restricted to an experimental design that comingled an effect of time with depth (i.e., the two depths were tested in separate months), necessitated by the logistical challenges of simultaneously establishing an *in situ* experiment at two depths. While we cannot exclude the possibility that time confounded the test of depth, the potential influences of this effect were reduced by stringently standardizing protocols between months, sampling larvae from colonies on the same lunar day of each month [as larval phenotype differs among release days in brooding corals (Cumbo et al., 2013)], using new colonies each month (i.e., they were statistically independent), and testing for differences in ambient seawater temperature between months. With an understanding of the limitations of the study, the present results have relevance in evaluating the likelihood of ocean acidification to modify the dispersal and connectivity of reef corals among populations that are part of a larger metapopulation (Levin, 2006). For larvae of brooded corals, the impacts of high pCO$_2$ on the physiology, behavior, and response to physical conditions suggests it will be productive to consider these effects in order to evaluate the potential for larval dispersal in a more acidic ocean.

ANIMAL RIGHTS STATEMENT

All known animal care and ethics issues for invertebrates were followed.

AUTHOR CONTRIBUTIONS

JB and PE planned the experiments. JB conducted the experiments. JB, SH, and HK contributed to the experiments. JB analyzed the data with advice from PE. JB and PE wrote the manuscript with contributions, review, and editing from SH and HK.

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frontiers in Marine Science

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How Life History Characteristics and Environmental Forcing Shape Settlement Success of Coral Reef Fishes

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Larval settlement is shaped by the interaction of biological processes (e.g., life history strategies, behavior etc.) and the environment (e.g., temperature, currents etc.). This is particularly true for many reef fishes where larval stages disperse offshore, often spending weeks to months in the pelagic realm before settling to shallow-water reefs. Our ability to predict reef fish settlement and subsequent recruitment and population dynamics depends on our ability to characterize how biological processes interact with the dynamic physical environment. Here we develop and apply an individual-based model that combines biological processes with high-resolution physical forcing to predict larval fish dispersal and settlement over time and space. Our model tracks individual larval fish from spawning to settlement and allows for the inclusion of biologically relevant stochasticity (individual variability) in modeled processes. Our model is also trait-based, which allows individuals to vary in life history characteristics, making it possible to mechanistically link the resulting variability in settlement probabilities to underlying traits such as spawning date and location, pelagic larval duration (PLD), body morphology, etc. We employ our biophysical model to examine how biology interacts with the physical environment to shape settlement predictions for reef fish off western and southern Hawaiʻi Island. Linked to prevailing surface currents, we find increased probabilities of settling associated with shorter PLDs and fish spawned in southern and southwestern locations. Superimposed on this, eddies, common to leeward Hawaiʻi Island, offer a second pathway to successful settlement for individuals with longer PLDs, particularly for fish spawning in summer months. Finally, we illustrate how lunar-timed spawning as well as morphological features (e.g., fin and head spines) may impact settlement success by altering the mortality landscape experienced by larvae. This work identifies life history characteristics that predict the self-recruitment pathways necessary for population persistence for the relatively isolated Hawaiʻi Island. Our results can be used to develop future hypotheses regarding temporal and spatial variation in recruitment for reef fishes on Hawaiʻi Island and beyond.

Keywords: early life history, settlement, recruitment, pelagic larval duration, reef fish, individual-based model, connectivity, Hawaiʻi Island

INTRODUCTION

A large variety of marine invertebrates and fishes begin life with a planktonic larval stage. Coral reef fishes are typical in this respect, and larvae often spend weeks to months in the pelagic realm before settling back to the reef as new recruits (Lester and Ruttenberg, 2005). Survival and dispersal during this vulnerable planktonic stage will influence population connectivity, as well as production and viability of adult populations (Houde, 2009). Self-recruitment is critical for the replenishment of reef fish populations that are not likely to receive recruits from other populations, such as the Hawaiian Islands (Toonen et al., 2011). Hawaiʻi Island is located at the southern end of the Hawaiian archipelago. Major surface currents in the Hawaiian archipelago include the westward flowing North Equatorial Current that bifurcates around Hawaiʻi Island to result in northward flowing currents up the archipelago (e.g., Hawaiian Lee Current, North Hawaiian Ridge Current, Lumpkin, 1998, **Figure 1**). The prevailing currents as well as Hawaiʻi Island's position at the southernmost end of the archipelago means that this island likely relies on self-recruitment for population persistence and may act as an important source of larvae for islands downstream (Wren et al., 2016). Indeed, self-recruitment has been measured via parentage analysis for reef fish on this island (e.g., lauʻipala or yellow tang, *Zebrasoma flavescens;* Christie et al., 2010).

The return of young fish to reefs after spending time in the plankton (i.e., "settlement" leading to "recruitment," or the observation of a newly arrived juvenile in the adult habitat, Caley et al., 1996) can be influenced by a variety of biological and physical factors (Victor, 1983; Jones et al., 2005; Puritz et al., 2016). Interactions between a fish's life history characteristics (e.g., birth date, larval morphology, pelagic larval duration or PLD) and the physical environment such as temperature (Balch et al., 1999), food availability (e.g., phytoplankton abundance, Polovina et al., 2001; Platt et al., 2003) and currents (e.g., cyclonic eddies, Fox et al., 2012; Pusack et al., 2014) result in within- and between-species variations in production, connectivity and recruitment. For example, an individual's location and date of birth selects the state of the environment to which they are exposed during pelagic development, including their advective environment, as well as the temperature, food and mortality landscape. An individual's PLD controls the length of time they are exposed to the pelagic environment, and influences their ability to disperse and find suitable reef habitat. In addition, morphological features can influence both the costs of development as well as how larvae experience factors such as mortality during development (Sogard, 1997). For example, larval development of elongate fin and head spines found in a number of reef fish species may reduce size-selective mortality by gape-limiting predation (e.g., Moser, 1981; Price et al., 2015), thereby allowing fish with spine morphology to successfully exploit areas with higher predator densities.

These interactions between larval biology and the physical environment cause inter-annual variation in settlement and recruitment, and they ultimately influence the production and persistence of the resulting adult population (Houde, 2009). Moreover, these biophysical dynamics will shape dispersal and connectivity, as well as the potential for local adaptation (Warner, 1997). Identifying the mechanisms and outcomes regarding these biophysical interactions can help us explain production and population dynamics in coral reef ecosystems. In this contribution, we tested the hypothesis that variation in biological characteristics of birth date, birth location, PLD, and spine morphology result in variations in predicted settlement probabilities for reef fish off the western and southern coasts of Hawaiʻi Island. To test this hypothesis, we developed and applied an individual-based model (IBM) that included a range in life history strategies forced by high-resolution hydrodynamic estimates of the ocean state for the region generated by the Regional Ocean Modeling System (ROMS). We followed individuals from spawning to settlement and explored the resulting trajectories and settlement success with respect to their individual life history traits. In so doing, we identified biophysical pathways influencing settlement probability and how these biophysical interactions may explain observed patterns in reef fish life histories.

MATERIALS AND METHODS

We developed a stage-based model that tracks individuals from spawning, through egg and larval stages, to settlement. Our IBM links biological traits to the physical environment similar to previous IBM modeling tools (e.g., Paris et al., 2005, 2013; North et al., 2008; Banas et al., 2009; Gilbert et al., 2010; Neuheimer et al., 2010; Bidegain et al., 2013), while also allowing for individual variability in life history strategies (e.g., birth date, location, PLD, and morphology) to test the influence of life history variability on settlement probability. Moreover, our model set-up exploits the "individual" in individual-based modeling to track individuals representing all combinations of life-history traits tested. This approach allows us to quantitatively compare effects of different life history traits (e.g., spawning location vs. PLD) on settlement success, as well as consider interactions among effects (e.g., spawning date and PLD). The model followed a population matrix through time where each row was an individual and columns tracked physiological and ecological metrics as the fish moved through time and space (following Neuheimer et al., 2010). The model was initially parameterized with spawning sites and life history traits to represent a range of Hawaiian reef fishes, but at times used values specific to lauʻipala or yellow tang (*Z. flavescens*), one of the better studied species in this region (e.g., Table S1 for further details).

The model was initialized with one female at each of seven known spawning locations spanning the western and southern coasts of Hawaiʻi Island (**Figure 1**, Table S1; based on Christie et al., 2010). At each time-step (2 h), the population evolved based on stage-dependent reproduction, development, growth, transport, and mortality. A time-step of 2 h allowed for a balance between computational efficiency and the high-resolution temporal and spatial physical forcing (see also section Transport below). All modeling and data analysis was done in the programming language R (R Core Team, 2016).

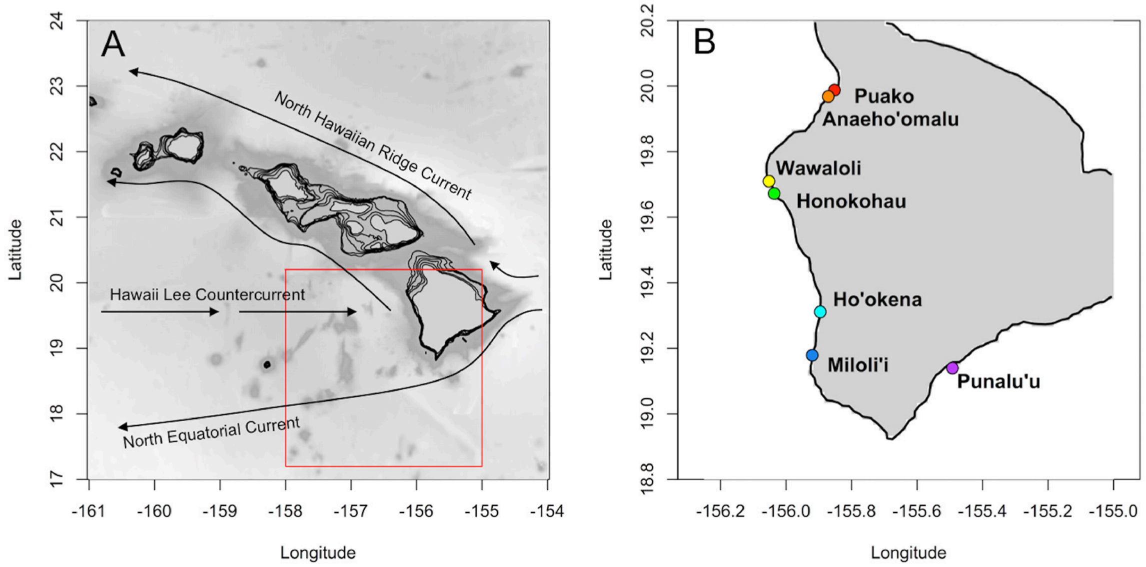

FIGURE 1 | (A) Main Hawaiian Islands with major surface currents (after Lumpkin, 1998). Model domain denoted in red. **(B)** Hawai'i Island with spawning locations (colors) as in Table S1.

Reproduction

At each time-step, individuals were spawned into the larval population. As our intention was not to investigate effects of fecundity characteristics on settlement success, individuals were added to the population based on a constant mean daily number of eggs chosen to be (i) large enough to provide a population of individuals to represent modeled life history trait variability, (ii) small enough to keep computations tractable, and (iii) realistic regarding observed variability in egg production rates among reef fishes. We used an estimate of 425 eggs female^{-1} day^{-1}, which was measured for bluehead wrasse (*Thalassoma bifasciatum*) in the Florida Keys (Holt and Riley, 2001) and is within the range of daily egg production rates for other species and locations (e.g., between 44 and >24,000 eggs female^{-1} day^{-1} for *Z. flavescens* off Hawai'i Island, Bushnell et al., 2010).

Individuals were spawned at every time-step and each of seven spawning locations (**Figure 1**, Table S1) to test the respective influence of birth date and spawning location on the probability of settlement. At spawning, new individuals (rows) were added to the population (matrix) representing the total number of individuals spawned. Their birth date (current time-step) and location (based on their mother) were recorded. We restricted our analyses to pelagic spawners with buoyant eggs (excluding demersal spawners), as these represent the majority of reef fish species (Thresher, 1984; Leis and Carson-Ewart, 2001; Luiz et al., 2013). Individuals were assigned an egg hatch time chosen from a uniform distribution between 24 and 48 h (Thresher, 1984). Each individual was also assigned a PLD sampled from a uniform distribution between 25 and 100 days. This PLD range represents observed PLDs for a range of pelagic spawning reef fish species (e.g., 25–90 days for Hawaiian endemics; Lester and Ruttenberg, 2005; Luiz et al., 2013), allowing us to assess the influence of PLD on settlement success. Spawned eggs are assigned a depth of 2 m to represent the positive buoyancy of eggs for the majority of reef fishes (Thresher, 1984; Colin and Clavijo, 1988) and based on field observations from Walsh (personal communication). In addition, individuals were randomly assigned spine morphology with presence or absence of elongate fin or head spines (50% probability of spine) allowing us to test the indirect influence of morphological changes on settlement probability (see also section Mortality). Eggs were assumed to be fertilized with 100% success (see section Discussion). Hereafter, "egg" refers to fertilized egg or zygote.

Development

At each time-step, egg age was compared to the individual's hatch time and eggs that were estimated to have hatched (i.e., age ≥ hatch time) were relabeled as larvae and assigned a larval depth. Larval depth was chosen from a Poisson distribution with a λ of 28 m (based on observed vertical distribution of larvae in Hawai'i; Boehlert and Mundy, 1996; Wren et al., 2016) and was restricted to the available advection depth layers (see section Transport). For all larvae, age was compared to the individual's PLD to identify those that were expected to have settled within the time-step. Settled individuals were marked settled, recorded along with their location at settlement, and then removed from the population matrix at the beginning of the next time-step.

Growth

An estimate of individual size (total length) was needed to assess size-dependent mortality risk. Length at hatching was set at 1.5 mm (Leis and Carson-Ewart, 2001). Once hatched, individuals started growing at a constant growth rate of 0.037 mm hr^{-1}; an estimated growth rate based on a settlement size of 50 mm (Leis and Carson-Ewart, 2001; Claisse et al., 2009) and PLD of 55 days (Christie et al., 2010) for *Z. flavescens*. Size at settlement ranges from 7 to 75 mm for a range of coral reef perciform fishes (Leis and Carson-Ewart, 2001).

Transport

At each time-step, all non-settled individuals were transported based on their geographic location-specific and depth-specific advection. Swimming behavior was not included in the current study but could be defined in future efforts where information on swimming speed and directionality exists (see also section Discussion). Advection estimates were obtained from a Regional Ocean Modeling System (ROMS) model developed and operated for waters around the Hawaiian Islands (Souza et al., 2015). The ROMS model assimilates daily, real-time data from satellites, autonomous gliders, Argo drifters, ship measurements, real-time high-frequency radar, and other data of opportunity. For this study, a 1 km high-resolution ROMS model was nested within the 4 km operational model described in Souza et al. (2015). We limited the larvae to the upper 100 m of the water column, which is represented by 16 depth layers: 2 m, every 5 m from 5 to 50 m, and then every 10 m from 50 m until 100 m. The ROMS model provides physical forcing estimates (current velocity and temperature) on an hourly time-step. The influence of biology on transport was included through birth date, birth location, PLD, spine morphology, and the stage-specific depth distributions described above.

At each time-step, the time-specific advection (u: m s^{-1}: east-west or zonal component; v: m s^{-1} north-south or meridional component), for each individual was estimated via a 4th order Runge-Kutta method. Advection estimates on the ROMS grid were interpolated to each individual's location based on a two-dimensional barycentric interpolation. The distance traveled in the zonal direction at each time step was added to the current longitude to determine east/west movement ($u \cdot \Delta t$). The distance traveled in the meridional direction at each time step was added to the current latitude ($v \cdot \Delta t$) to determine the individual's new latitude. Distances were corrected for the spherical shape of the Earth. Any individual estimated to have moved onto land was placed back to its last position in the ocean. To allow for sloping coastal bathymetry, individuals moving to locations shallower than their current depth were reassigned to the depth-layer closest to the bottom depth at their new location. Individuals leaving the model domain were removed from the population.

Mortality

Individuals were removed from the population based on size-dependent and spatially varying mortality rates (and resulting survival probabilities, Figure S1). Mortality rate decreased with increasing size to represent general patterns of declines in predation with increasing size in the ocean (e.g., Landry, 1976; Bailey, 1984; Dekshenieks et al., 1997[1], Figure S1A). Mortality rate also decreased with bottom depth to represent the decrease in visual predators with depth in pelagic waters (e.g., following Dekshenieks et al., 1997, Figure S1B), particularly as vulnerable larvae move away from the more densely populated communities of potential predators on the reef. In both cases, mortality functions were chosen such that estimates of the integrated mortality rates did not differ significantly from that of a constant mortality rate ($m_{constant}$, see below) based on the number of recruits per female (following Dekshenieks et al., 1997; Figure S1). At each time-step (t), the survival probability of each individual (i) was estimated as:

$$S_{i,t} = e^{(-m_{i,t} \cdot \Delta t)} \tag{1}$$

where the mortality rate for individual i and time-step t ($m_{i,t}$) was

$$m_{i,t} = m_{constant} \cdot e^{(-0.007 \cdot Depth_{i,t} + -0.2 \cdot Length_{i,t})} \tag{2}$$

based on the constant mortality estimate ($m_{constant}$, Table S1), $Depth_{i,j}$ is the bottom depth at the individual's location (m) and $Length_{i,j}$ is the individual's effective length (mm). The instantaneous mortality rate ($m_{constant}$) was obtained from the observed annual survival probability (S_{year}, dimensionless) of 100 individuals from 155,125 eggs $female^{-1}$ (425 eggs $female^{-1}$ day^{-1} × 365 days):

$$S_{year} = \frac{100}{155125} = 0.00064 \tag{3}$$

and converted to a constant mortality estimate ($m_{constant}$) with:

$$m_{constant} = (-\log_n S_{year}) \cdot \left(\frac{1\ hr}{365\ days \cdot \frac{24\ hr}{1\ day}} \right). \tag{4}$$

This approach led to a constant mortality rate of 8.4×10^{-4} hr^{-1} or 2.0×10^{-2} day^{-1}; an estimate within the range of natural mortality estimates for fish egg and larval stages across species ($\sim 10^{-1}$-10^{-2} day^{-1}; McGurk, 1986). Effective length was defined as egg size for egg stages (Table S1) and was defined by larval size and spine morphology for larval stages. The latter allowed us to include possible size-dependent mortality (predation) reduction for those fish exhibiting spines to make themselves effectively bigger (i.e., reducing gape-dependent predation, Fuiman and Magurran, 1994). Presence of a spine increased the effective length of individual larvae by 40%, a value within the range of relative spine length for reef fish larvae (e.g., gray triggerfish, *Balistes capriscus*, exhibiting spine lengths ranging from 7 to 50% of fork length during larval development; Matsuura and Katsuragawa, 1981). Each individual's fate was determined by sampling from a binomial distribution (1 = survive) based on their $S_{i,t}$.

Model Simulations

The focus of this analysis was on intra-annual changes to the probability of successful settlement success. Individuals were modeled for January 2011 through December 2013, representing typical (between-ENSO) years. Three separate model runs were simulated, each for the complete time period (2011–2013), and run results were consolidated to minimize stochastic effects on model results. The population matrix was stored at each time-step with output including individual larval trajectories, as well

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[1] Prior to 2002 MA McManus published as MM Dekshenieks.

as information on individual fish traits (e.g., birth date, year, birth location, PLD, spine morphology).

While no trade-offs in traits (e.g., spawning date, location, PLD, spine) were explicitly assigned, trade-offs due to life history strategy were implicit. For example, PLD varied among individuals. This in combination with size-dependent mortality and invariable growth rates meant shorter-PLD individuals experienced higher mortality at settlement size than those with longer PLDs.

Statistical Modeling

We used model output to test the hypothesis that variability in the settlement success of individuals back to Hawai‘i Island is explained by a suite of life history characteristics (i.e., birth date and location, PLD, and body morphology). Here, the binomial settlement result (*Settled*) is recorded as successful when an individual is within the 50 m depth contour of Hawai‘i Island at time of settlement (i.e., when $age_{i,t} \geq PLD_i$). Reef fish are found continuously along the west Hawai‘i Island coast and, besides depth-dependence, habitat suitability is considered constant across our model domain. Future studies exploring e.g., benthic invertebrates requiring particular substrate for settling could expand on the definition of habitat suitability modeled here.

For our purposes (focus on Hawai‘i Island self-recruitment), we did not consider individuals that may settle outside the model domain (addressed in the Discussion). We assessed the hypothesis that settlement back to Hawai‘i Island (*Settled*) is explained by variability in life history traits: birth date (*BirthDay*), *PLD*, and morphology (i.e., presence/absence of a spine, *Spine*). Attempting to identify possible mechanisms behind temporal variations in settlement probability, we also included information on tidal height (*Tide*, m) and moon phase (*Moon*). The former was obtained for the Kawaihae, Hawai‘i station from the National Oceanic and Atmospheric Administration’s (NOAA) Center for Operational Oceanographic Products and Services. In the latter, birth dates were labeled “New” or “Full” when they were within ±3 days of the new or full moons, respectively, or “Other” if otherwise. We also tested sensitivity of statistical results to this moon phase definition by re-assessing model results with days labeled “New” or “Full” when birth dates were ±1 or 5 days of the new or full moons (else days are labeled “Other,” as above). Finally, though the focus of this analysis is on intra-annual and island-scale changes to settlement probability, we included possible variations across years and spawning locations by including birth year (*BirthYear*) and spawning location (*Location*) as predictors.

The response ($Settled_i$) was modeled as observations from a binomial distribution (successful vs. unsuccessful settlement back to Hawai‘i Island):

$$Settled_i \sim B\left(n_i,\ \pi_i\right) \tag{5}$$

$$E\left(Y_i\right) = n_i \cdot \pi_i \qquad mean(expected)value \tag{6}$$

$$\operatorname{var}\left(Y_i\right) = n_i \cdot \pi_i \cdot \left(1 - \pi_i\right) \qquad variance \tag{7}$$

where the number of trials (binomial denominator) is $n_i = 1$ (independent trials, i.e., a Bernoulli distribution) and the probability is π_i. The probability (π_i) was modeled as a function of our predictors using a generalized additive model (GAM):

$$\begin{aligned} g\left(E\left(Y_i\right)\right) = \ & g\left(\pi_i\right) \sim f\left(BirthDay_i,\ PLD_i\right) + \ Spine_i \\ & + Location_i + \ Moon_i + f\left(Tide_i\right) + \ BirthYear_i \end{aligned} \tag{8}$$

including non-linear effects of continuous variables *BirthDay*, *PLD*, and *Tide*, in addition to interactions between *BirthDay* and *PLD* through a tensor product smoother. Effect of *BirthDay* was fit with a cyclic cubic spline to allow for the cyclical nature of the predictor (i.e., 31 December and 1 January are adjacent), while effects of *PLD* and *Tide* were both fit with thin plate splines. Linear effects were included for *Spine* (categorical with two levels as “absence” or “presence” of spine, see previous Methods), *Moon* (categorical with three levels as “New,” “Full,” or “Other,” see previous Methods), *Location* (categorical with 7 levels for locations, **Figure 1**, Table S1) and *BirthYear* (categorical with three levels as 2011, 2012, and 2013). Further interactions among predictors (e.g., *Location* and *PLD*) were not within the scope of our analysis but could be included in the future to test additional hypotheses, e.g., investigations into the spatial variability in life history characteristics of successful settlers.

The link function, $g\left(\pi_i\right)$ provides the relationship between the expected value of the response and the linear predictor. The canonical logit link function was originally employed:

$$g\left(\pi_i\right) = logit\left(\pi_i\right) = \log_e\left(\frac{\pi_i}{1 - \pi_i}\right). \tag{9}$$

As alternative link functions may increase model performance, we also fit our model using alternate link functions of probit:

$$g\left(\pi_i\right) = probit\left(\pi_i\right) = \Phi^{-1}\left(\pi_i\right), \tag{10}$$

where Φ is the standard normal distribution function, and the complementary Log-Log (cloglog) link:

$$g\left(\pi_i\right) = cloglog\left(\pi_i\right) = \ \log_e\left(-\log_e\left(1 - \pi_i\right)\right), \tag{11}$$

and assessed model results.

The GAM was fit using the *bam()* function from the mgcv package in R, which eases GAM fits for very large datasets (Wood, 2011). While GAMs are somewhat robust to predictor collinearity issues, pairwise correlation among all predictor combinations was assessed prior to model fitting. Inspection of residuals and comparisons of explained deviance were used to test model validity and select among non-nested models (e.g., among link functions). In addition, the level of complexity (basis dimension) of the smoothers was assessed by examining residual variance of near neighbors compared to overall residual variance (i.e., the k index, following Wood, 2011). Model selection based on a ranking of both Akaike’s Information Criterion (AIC) and Bayesian Information Criterion (BIC) was used to compare across a set of (nested) candidate models. AIC favors the predictive power of the models while BIC includes harsher penalties for complex models, making the latter useful for identifying important processes (predictors) underlying the explained deviance, particularly when sample sizes are large (Efron and Hastie, 2017). While an exhaustive model selection (including all possible predictor combinations) was not possible due to the large sample size, the candidate model set allowed us to assess the importance and likely nature (shape, interactions) of each predictor's effects (Table S2). Once the best-specified model was chosen, explained deviance was partitioned among predictors by refitting the model reduced by one predictor at a time while maintaining the estimated smoothers from the best-specified model.

RESULTS

In total, 9,683,781 individuals were tracked over the three model runs, with a total of 56,702 fish (0.585%) successfully settling to western and southern Hawaiʻi Island. **Figure 2** shows examples of simulated trajectories for successful settlers.

There were no significant pairwise correlations between predictor pairs, with all correlation estimates being <0.0074; the highest pairwise correlation was expectedly between *Moon* and *Tide* at 0.0074. The starting model (with logit link, Equation 9) explained 19.2%, of the overall deviance in settlement probability. A switch of link functions to probit (Equation 10) increased explained deviance to 19.7% and resulted in slightly better-behaved residuals (though departures from normality were found, and expected given the large sample size and low probability of settling, e.g., Augustin et al., 2012). Following this, a set of candidate statistical models assembled to test model structure and predictor importance were fit using the probit link function (Table S2). Models in the candidate model set were ranked by both AIC and BIC. Two models were favored via BIC comparisons (i.e. models within $\Delta\text{BIC} < 2.14$ of lowest):

$$probit\,(\pi_i) \sim f\left(BirthDay_i,\ PLD_i\right) + Spine_i + Location_i \tag{12}$$

$$probit\,(\pi_i) \sim f\left(BirthDay_i,\ PLD_i\right) + Spine_i + Location_i + Moon_i \tag{13}$$

with a BIC weight of 74.5 and 25.5% for Equations (12, 13), respectively (Table S2). These models included non-linear and interaction effects of *BirthDay* and *PLD* as well as linear effects of *Spine*, *Location,* and in one model (Equation 13) *Moon*. AIC ranking included these models in the top 55% of models, ranking the more complicated starting model (Equation 8) as the top model with an AIC weight of 100% (Table S2). The addition of these extra predictors in the AIC top model did not add a significant amount to the overall explained deviance (+0.006%) and we chose Equation (13) as our best-specified model, explaining 19.7% of the overall deviance in settlement probability.

Probability of settling varied significantly across birth locations, explaining the highest proportion (15%) of the total overall explained deviance (**Table 1**). The greatest probability of settling occurred for fish born on the south coast at Punaluʻu ($4.7 \times 10^{-2} \pm 6.2 \times 10^{-4}$) with all other sites associated with an order of magnitude lower probability of successfully recruiting (1.7×10^{-3}-8.7×10^{-3}, **Table 1**). Fish born in the second most southerly location (Miloliʻi) had the second highest probability of settling ($8.7 \times 10^{-3} \pm 1.7 \times 10^{-4}$), while individuals born at Puako and Anaehoʻomalu in the north and Hoʻokena on the southwest coast were associated with similar probabilities of settling ($\sim 2.4 \times 10^{-3}$, **Table 1**).

The non-linear and interacting effects of *BirthDay* and *PLD* explained 4.6% of the overall deviance with ∼4.1% attributable to *PLD* and ∼0.64% to *BirthDay* (**Table 1**, **Figure 3**). Including both non-linear and interacting effects increased model performance (Table S2). Throughout the year, those larvae with the shortest PLDs (e.g., 25 days) had the highest probability of successfully settling (**Figure 3**). For fish with longer PLDs (e.g., >50 days), probability of settling increased from a minimum in winter months (December–January) to a maximum in the summer (June for PLDs of 75–100 days) or fall (August/September for PLD = 50 days, **Figure 3**). Median PLD of individuals successfully settling was highest during typical reef fish spawning seasons (i.e., 15 January through 15 October; Walsh, 1987, see section Discussion, **Figure 3**, Figure S1). Due to the range of PLDs modeled, size at settlement ranged between 22 and 89 mm, similar to observed size at settlement of coral reef perciform fishes (7–75 mm, Leis and Carson-Ewart, 2001).

Effects of spine morphology explained 0.7% of the overall deviance in probability of settling, with higher probability of successfully settling for fish with a spine than without ($P < 0.0001$). Effects of moon phase during spawning (*Moon*) appeared in only one of the top two models, explaining 0.0044% of overall deviance in settlement probability. Moon effects were significant only when model phase was defined ±3 days of the new or full moons; predictors estimated with definitions of ±1 day or ±5 days were not significant (based on AIC and BIC model ranking). Effects of moon phase estimated fish born under a new moon phase had a probability of settling of 0.047 ($\pm 6.2 \times 10^{-4}$ standard error), which was slightly (0.001) but significantly higher than fish born under Full ($P = 0.0027$) or Other ($P < 0.001$) moon phases. There was no difference in probability of settling between fish born under Full vs. Other moon phases ($P = 0.30$, **Table 1**).

DISCUSSION

Our results demonstrate how life history characteristics (e.g., location of birth, birth date, PLD, body morphology) can interact with the physical environment to affect the probability of reef fish settlement, using western and southern Hawaiʻi Island as a case study.

Physical Challenges "Select" for Biological Characteristics

Successful settlement back to Hawaiʻi Island is necessary for population persistence especially considering the remoteness of the Hawaiian archipelago. In particular, Hawaiʻi Island represents the southward limit of the archipelago with surface currents generally flowing northwestward toward the rest of

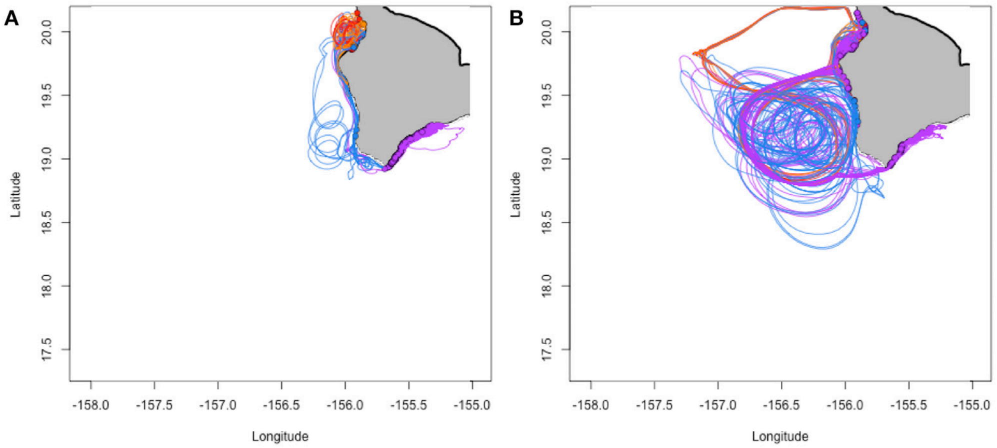

FIGURE 2 | Example trajectories for successfully settling individuals in February (**A**; 962 individuals) and May (**B**; 215 individuals) of 2012. Colors correspond to spawning locations in **Figure 1B**, Table S1.

TABLE 1 | Results of the best-specified model (Equation 13) including % explained deviance by each predictor as well as probability of settling estimates.

Predictor	Explained deviance (%)	Predictor level	Predicted probability of settling (± standard error)
Location	15	Puako	$2.5 \times 10^{-3} \pm 7.2 \times 10^{-5\wedge}$
		Anaeho'omalo Bay	$2.4 \times 10^{-3} \pm 6.9 \times 10^{-5\wedge}$
		Wawaloli Beach	$1.7 \times 10^{-3} \pm 5.5 \times 10^{-5}$
		Honokohau	$1.9 \times 10^{-3} \pm 6.1 \times 10^{-5}$
		Ho'okena	$2.3 \times 10^{-3} \pm 6.8 \times 10^{-5\wedge}$
		Miloli'i	$8.7 \times 10^{-3} \pm 1.7 \times 10^{-4}$
		Punalu'u	$4.7 \times 10^{-2} \pm 6.2 \times 10^{-4}$
f(BirthDay, PLD)	4.6 (*PLD:* 4.1%; *BirthDay:* 0.64%)		See **Figure 3**
Spine	0.71	Present	$4.7 \times 10^{-2} \pm 6.2 \times 10^{-4}$
		Absent	$2.8 \times 10^{-2} \pm 4.1 \times 10^{-4}$
Moon	0.0044	New	$4.7 \times 10^{-2} \pm 6.2 \times 10^{-4}$
		Full	$4.6 \times 10^{-2} \pm 6.0 \times 10^{-4*}$
		Other	$4.5 \times 10^{-2} \pm 5.2 \times 10^{-4*}$

For predicted probability of settlement, non-target predictor variables are held constant at Location = Punalu'u, BirthDay = 218, PLD = 50 days, Spine = Present, Moon = New as needed. Similar symbols (or ^) indicate predictor levels resulting in similar probability of settling estimates (P > 0.026).*

the main Hawaiian Islands (**Figure 1**). Because of this general northwestward flow, individuals born in the more southerly spawning locations (Punalu‘u and Miloli‘i) had the highest probability of settling back to the western and southern coast of Hawai‘i (e.g., 4.7×10^{-2} and 8.7×10^{-3} probability of settling, respectively, when other factors held as per **Table 1**), while fish born in more northerly locations had a high probability of being advected out of the model domain (e.g., 1.7×10^{-3} probability of settling when spawned at Wawaloli Beach and other factors held as per **Table 1**). Christie et al. (2010) provide empirical data consistent with these predictions for yellow tang (*Zebrasoma flavenscens*). While fish lost through this northern model boundary did not contribute to self-settlement on Hawai‘i Island, they may represent a source of larvae for other populations in the Hawaiian archipelago. Spawning location explained the most variability (deviance) in settlement success (15% of explained deviance) in our model, followed by PLD (4.1% of explained deviance; **Table 1**). Regarding the latter, short PLDs were associated with higher probabilities of settling—again, allowing fish to settle before they are advected out of the model domain (**Figure 2A**, **Table 1**). Short PLDs may be particularly advantageous in the southwest of Hawai‘i Island where steep bathymetry means fish do not need to go far to escape high-predation shallow waters (more on mortality in the text that follows).

Superimposed on top of this general surface current pattern, cyclonic, and anticyclonic eddies are common on the leeward side of Hawai‘i Island (Qiu et al., 1997). These eddies offer a

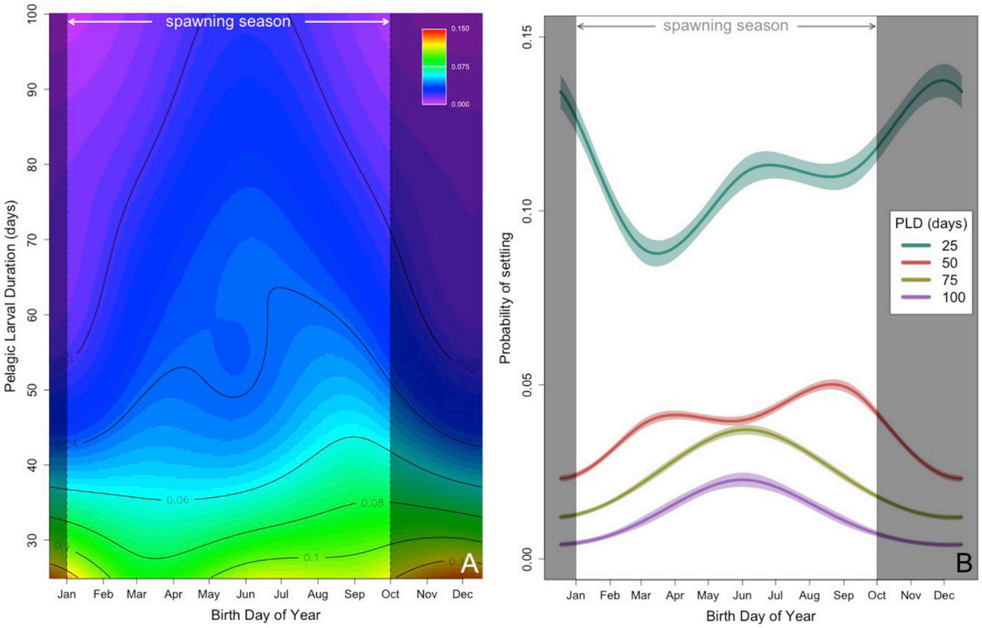

FIGURE 3 | (A) Predicted probability of settling (contours and color scale), from high (red) to low (purple) probability, as a function of birth date (x-axis, *BirthDay*) and *PLD* (y-axis, days). **(B)** Predicted probability of settling (±2 standard error) as a function of birth day of year (*BirthDay*) and *PLD* (days, colors, with green = 25 days, red = 50 days, yellow = 75 days, and purple = 100 days). In both panels, times outside the common spawning season are shaded in gray (Walsh, 1987; see section Discussion). Other predictors are held constant at *Location* = Punalu'u, *Spine* = present, *Moon* = New.

mechanism for reef fish (particularly those with longer PLDs, Christie et al., 2010) to develop and grow away from nearshore high predation waters while at the same time provide a path back to the reef for settlement when larger (Lobel and Robinson, 1986). A similar hypothesis was offered for juvenile anchovies, which move away from higher densities of predators on the shelf where they are spawned in the Bay of Biscay to offshore waters with lower densities of predators for their development period (Irigoien et al., 2007). Reef fishes seem to be "using" these eddies: mean abundances of fish larvae were found to be 4× higher in an eddy (34.9/1,000 m^3) compared to the same waters before eddy formation (8.8/1,000 m^3; Lobel and Robinson, 1986). Moreover, larval fish distribution within eddies was shown to be stage-specific, with eggs and post-hatchling larvae more abundant near the eddy core and late-stage larvae more abundant in the outer edge of the eddy (Lobel and Robinson, 1986). Off the west coast of Maui, Hawai'i, Storlazzi et al. (2006) concluded that persistent small-scale eddies may help to retain coral larvae during the summer spawning season. Regardless of eddy size, it is possible that some larvae are able to actively respond to the eddy gradient allowing them to control the length of residence in the eddy and leave the eddy when it is time to settle (McManus and Woodson, 2012). In addition to retention mechanisms that help to maintain larvae close to original or nearby islands, eddies may also allow for faster growth by providing increased food resources or temperatures and thus likely higher survival of the larvae (Shulzitski et al., 2016, 2017).

Not all eddies are created equal: mesoscale eddies are often advected westward or northwestward, sometimes rapidly; thus resident larvae can be carried far from land before they have a chance to fully develop. The ultimate destinies of these larvae will be determined by the direction and velocity of the eddy and of the currents into which they are released when the eddy eventually dissipates. Indeed, it is the eddies that form and are positioned close to shore for extended periods of time that increase settlement probability for west Hawai'i Island (e.g., **Figure 2B**) vs. eddies that quickly move offshore, away from the coast, resulting in individuals being advected far away from suitable habitat (e.g., Figure S3). During their lifetimes, mesoscale eddies may move up to 350 km in a westerly or northwesterly direction at an average of 5.2 km day^{-1} (Patzert, 1969). For example, cyclonic eddy Opal moved rapidly southward by ∼165 km over several weeks, with an overall average displacement speed of ∼8 km day^{-1} moving away from the islands (Maiti et al., 2008).

The seasonal timing of transport mechanisms including eddies appears to be correlated with the typical summer spawning season. Most Hawaiian reef fishes exhibit minimum spawning in winter, with spawning increasing with increasing water temperatures and day length before declining quickly as maximum water temperatures are reached in late summer/early fall (Walsh, 1984, 1987; Lobel, 1989). While the fall decline in spawning may be related to decreased larval survival or inhibition of gametogenesis because of higher summer temperatures (Walsh, 1987), our model suggests that biophysical interactions also result in declines in settlement success in the fall for those fish exhibiting longer PLDs (**Figure 3**). It is during the summer months (particularly April through September) when the less advective mesoscale eddies (nearshore and relatively stable) develop along the coast, allowing for longer larval development times while being retained near suitable habitat (**Figure 2B**). These smaller scale nearshore eddy features have been regularly and predictably observed on other islands as well (Storlazzi et al., 2006). We present evidence that dispersal and retention of larvae can be governed by the rotation and movement of eddies, and that the seasonal formation of these eddies may help explain the observed spawning season. Similarly, Donahue et al. (2015) found modeled biophysical processes predicted higher larval settlement probabilities for fish spawned during the observed spawning season for lane snapper (*Lutjanus synagris*) in the Florida Straits. Thus, spawning strategies that allow larval development in offshore eddies may represent a "loophole" (Bakun and Broad, 2003; Irigoien et al., 2007) that allow fish to reduce mortality, resulting in recruitment and production pulses (e.g., Munch and Conover, 2004).

Our results offer two pathways, or biophysical mechanisms, that increase self-recruitment probabilities in western and southern Hawaii Island's advective environment: (i) develop quickly (short PLD) and avoid being advected away, or (ii) catch a ride on the "right" kind of eddy (allowing for longer PLDs). These pathways appear in our predicted settlement probabilities with probability of settling maximized for individuals with short PLDs in the winter months when the environment favors less retention (e.g., lower abundance of nearshore eddies, **Figures 2A**, **3**) and, for longer PLDs, in the summer months where nearshore eddies are more abundant (**Figures 2B**, **3**). Moreover, this range of potential strategies that favor larval survival and recruitment is found in the PLD-trait distribution of our modeled individuals with examples of successful settlers from the entire PLD model range (25–100 days) and a median PLD of 43 ± 13 days (median ± median absolute deviance; Figure S2). These PLD estimates coincide well with many of the common species of coral reef fishes in the Hawaiian Islands, which demonstrate considerable PLD variability across species (e.g., 8–70 days for west Pacific species, and 25–90 days for Hawaiian endemics; Lester and Ruttenberg, 2005).

Influences of the Mortality Landscape

The presence of a pelagic larval phase may act to increase survival probabilities in temporally, spatially, and developmentally variable mortality environments (Johannes, 1978). Settlement success (and ultimately survival) will depend on how life history characteristics (e.g., size, stage durations, and timing) result in larvae moving through this dynamic mortality landscape. Here we incorporate both spatially (depth-dependent) and size-dependent mortality, mimicking the high nearshore and size-selective predator environment experienced by many marine animals. In this way, larval survival will change both in space (e.g., with spawning location bathymetry controlling how quickly predation pressure decreases with distance from shore) as well as time (e.g., mortality risk declines as individuals age and grow). To further illustrate how size-selective mortality landscapes may select for certain life history characteristics, we mimicked the increase in effective size that the development of elongate fin and head spines provide in some reef fish larvae (Moser, 1981). Spines potentially reduce the probability of an attack by gape-limited predators and therefore act as a mechanical deterrent to predation (Moser, 1981; Morgan, 1989; Price et al., 2015; Greer et al., 2016). The effectiveness of spines as a means of reducing predation by planktivorous fish has been experimentally demonstrated in marine crab larvae (Morgan, 1989) and is often assumed in fish larvae (Moser, 1981; Greer et al., 2016). Indeed, higher predation on fish larvae with shorter spines has been documented (Moodie, 1972), with some species increasing spine length (and other armor) when predator abundance is high (Gross, 1978; Januszkiewicz and Robinson, 2007; Weber and Brown, 2012). Small increases in effective larval size may therefore have a disproportionately large effect in reducing predation by gape-limited predators (Moser, 1981). We illustrated how the presence of a spine can increase the probability of settling by 67%, by making the individual effectively larger and thereby lowering the size-dependent mortality (**Table 1**). This value will vary given the predator field and strength of size-dependence on mortality. This aspect of the model could be used in the future to explore mechanisms driving the large variation of reef fish larval body plans (McCormick and Molony, 1995; Price et al., 2015), as well as estimating trade-offs between the benefit of reduced predation with the cost of spination and potential reduction in swimming speed accompanying the body-form change. Similarly, this work could be extended to explore the effects of other size-related traits on settlement success, e.g., temperature-dependent growth (Houde, 1989), size at hatching, etc.

Many species of reef fish exhibit lunar spawning periodicity with spawning around the new and/or full moons (e.g., Johannes, 1978; Walsh, 1987; Domeier and Colin, 1997; Colin, 2011). Spawning around a new or full moon may facilitate the flushing of eggs away from shallow water by using outgoing spring tides that are associated with these moon phases and quickly increasing the distance between the egg and potential predators on the reef (Johannes, 1978). Tropical reef fish have been observed spawning during an ebbing tide during which eggs are transported off the reef and away from planktivorous fish predators (James et al., 2002). Here we found that the probability of successful settlement is enhanced during new moon phases, however no significant effect of tidal height was observed. Empirically, Claisse et al. (2011) found no correlation between daily spawning movements of yellow tang and lunar cycles. Future efforts will explore other possible tidal measures (e.g., velocities) that may be underlying the higher settlement success for fish born around new moons. Note that avoiding visual predators under the cover of darkness has been hypothesized to explain settlement during new moons (Johannes, 1978). More broadly (beyond our model), the high incidence of lunar-timed spawning observed in the field may allow for reduced egg predation by spawning under low light levels and/or predator swamping (Johannes, 1978; Walsh, 1987), or may maximize fertilization success via spawning synchronization (Walsh, 1987).

Future Directions

These results motivate a number of future hypotheses that can be explored to explain biophysical forces shaping reef fish recruitment and survival. Our modeling tools can be used to examine spatial variability in life history characteristics (e.g., trait-based community structure) as well as connectivity pathways among local adult populations, both within Hawaiʻi Island and beyond. Similar questions can be raised concerning the biophysical factors shaping inter-annual patterns of settlement and recruitment, particularly for longer time-series of physical forcing (e.g., exploring interactions between biology and climate oscillations including the El Niño Southern Oscillation, ENSO). In addition, model tools can be extended to include heritable trait profiles that can explore questions of life history strategy adaptations over space and time, with or without expected trade-offs in traits. Finally, our IBM can be extended to include characterizations of other biological processes (e.g., swimming behavior, Deksheniek s et al., 1996; Fiksen et al., 2007; Staaterman and Paris, 2013) as well as biophysical interactions such as patchiness, thermal and/or food controls on development (e.g., Dekshenieks et al., 1993) and light-dependent mortality (as above). In particular, our model may be extended to include characterizations of larval spatial patchiness to explore the role patchiness may play in increasing the effective mortality estimates for fish eggs and larvae (McGurk, 1986). Moreover, our tools and methods can be applied to address similar questions of biophysical controls on settlement success for benthic invertebrates also exhibiting biphasic life-histories (e.g., Gilbert et al., 2010).

SUMMARY

We show that fundamental biophysical interactions can result in variation in settlement probability for marine species displaying a pelagic larval stage. The flexibility of our IBM along with high resolution spatial forcing allowed us to identify life history characteristics (e.g., birth date and PLD) that will result in the highest probability of successful recruitment and thus long-term persistence of reef fish populations for Hawaiʻi Island. We also used our model to identify possible mechanisms for the life history characteristics observed in the field (e.g., how advection may help shape spawning season and lunar-linked spawning behaviors) and demonstrated how mortality landscapes can favor morphological features (e.g., spine morphology; Morgan, 1989; Dekshenieks et al., 1997). Our modeling tool synthesizes current knowledge on reef fish ecology to test hypotheses that can direct future field and lab research to explain population dynamics and how larval fish use biophysical mechanisms in ways that minimize advective loss of larvae (e.g., Shulzitski et al., 2017). Moreover, we can use the model in future analyses to identify important knowledge gaps (e.g., environmentally dependent development rates, spatially and temporally varying mortality) needed to explore reef fish adaptive strategies and associated coral reef ecosystem dynamics.

AUTHOR CONTRIBUTIONS

JW-A, AN, BP, and MH: Conceived of the study; JW-A, AN, and BP: Designed the study; BP: Provided high-resolution physical forcing estimates; JW-A and AN: Developed, implemented, and analyzed computational and statistical models; CC, JG, MH, MM, BP, and JW: Contributed data, theory, and interpretation; JW-A and AN: Drafted the article. All authors critically revised the article. All authors approved the final version of the article. Authorship order is by first-and-last-author-emphasis with middle authors alphabetized.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2018.00065/full#supplementary-material

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frontiers in Marine Science

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Larval Fish Swimming Behavior Alters Dispersal Patterns From Marine Protected Areas in the North-Western Mediterranean Sea

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Most demersal fishes undergo a dispersal phase as larvae, which strongly influences the connectivity among adult populations and, consequently, their genetic structure and replenishment opportunities. Because this phase is difficult to observe directly, it is frequently simulated through numerical models, most of which consider larvae as passive or only vertically migrating. However, in several locations, including the Mediterranean Sea, many species have been shown to swim fast and orient. Here we use a Lagrangian model to study connectivity patterns among three Mediterranean Marine Protected Areas (MPAs) and compare simulations in which virtual larvae are passive to simulations in which oriented swimming is implemented. The parameterization of behavior is based on observations for two groups of species of the family Sparidae: species with small larvae (i.e., 9–11 mm), displaying a maximum swimming speed of 6 cm s^{-1} and a pelagic larval duration of 13–19 days (e.g., *Diplodus annularis* L., *Oblada melanura* L.) and species with large larvae (i.e., 14–16 mm), displaying a maximum swimming speed of 10 cm s^{-1} and a PLD of 28–38 days (e.g., *Spondyliosoma cantharus* L.). Including larval behavior in the model (i) increased the overall proportion of successful settlers, (ii) enhanced self-recruitment within the MPAs, but also (iii) increased the intensity, and (iv) widened the export of eggs and larvae (recruitment subsidy) from the MPAs; overall, it significantly changed connectivity patterns. These results highlight the need to gather the observational data that are required to correctly parameterize connectivity models.

Keywords: fish larvae, behavior, swimming, connectivity, dispersal, mediterranean sea, marine protected areas, modeling

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INTRODUCTION

Many coastal fish species undergo a pelagic larval phase while adults generally have a restricted home range, leading most dispersal to occur during the larval phase (Gaines et al., 2007), even if it is not limited to this stage (e.g., Di Franco et al., 2015). Predicting recruitment in adult populations after this larval phase is a major challenge in marine ecology and for the sustainable management of marine resources. But it remains difficult because the factors determining larval dispersal and survival are not all identified (Cowen et al., 2007; Botsford et al., 2009). Various methods have been developed to study larval fish dispersal (Cowen et al., 2007) and showed that dispersal distances may reach hundreds of kilometers in some regions (Kinlan and Gaines, 2003) or be very limited, with surprisingly high self-recruitment rates, in others (Jones et al., 2005; Cowen et al., 2006; Gerlach et al., 2007; Almany et al., 2017). Among all methods, modeling is the only approach that enables tracking (virtual) larvae throughout their pelagic journey (North et al., 2009). Biophysical models therefore contributed largely to the understanding of larval dispersal and population connectivity (e.g., Truelove et al., 2017) and to the testing of marine protected areas (MPAs) networks efficiency (Mouillot et al., 2011). Today, the use of such models have generalized and some even succeeded in predicting the intensity of larval supply to coastal areas (Sponaugle et al., 2012).

Robust connectivity models are particularly required in the Mediterranean Sea because European Union regulations require to expand the network of Mediterranean MPAs by 2020. This network is currently small and not very effective (Mouillot et al., 2011). Throughout the French Riviera, in the North Western Mediterranean basin, fisheries are mostly traditional, coastal, and managed at a small scale (on the order of kilometers). Fishermen are actively implicated in the management of marine resources and the establishment of a no-take zone in Cap Roux (43.5°E, 6.9°N) on their demand proves their willingness to sustainably manage the marine resources they exploit. While this local management is laudable, it also stresses the need for using adequate tools to assess the efficiency of MPA networks at regional scale or to estimate the export of individuals toward exploited areas.

While biophysical models improved, the quantification of larval fish behavior also underwent major advances over the last two decades and it is now recognized that most settlement-stage larvae of tropical and temperate perciform fishes have strong swimming abilities, both in terms of speed and orientation (reviewed in Leis, 2006; see Faillettaz et al., 2017 for data on Mediterranean species). Oriented swimming was initially thought to be limited to coastal areas, where larvae may use odor (Paris et al., 2013), sound (Simpson et al., 2005) or both to detect favorable settlement habitats (Teodósio et al., 2016). Increasing observations now suggest that fish larvae may also orient in the open ocean using coast-independent cues such as the position of the sun (Mouritsen et al., 2013; Berenshtein et al., 2014; Faillettaz et al., 2015) or even the magnetic field (Bottesch et al., 2016; O'Connor and Muheim, 2017). These empirical observations were carried out in several regions and environments: Australia (Leis et al., 2014), Taiwan (Clark et al., 2005), North Sea (Cresci et al., 2017), Mediterranean Sea (Faillettaz et al., 2015) etc. They suggested that most perciform fish larvae have the means to orient at any spatial scale in the oceans using different mechanisms, which may have evolved to help them reach favorable settlement habitats (Paris et al., 2013; Leis et al., 2014, 2015; Bottesch et al., 2016).

It is noteworthy that nearly two decades ago, Jones et al. (1999) developed a numerical approach that suggested that active swimming might be necessary to explain the high self-recruitment rates they observed. Since then, several studies that included larval behavior in biophysical models found striking differences compared to simulations of passively drifting larvae (e.g., Paris and Cowen, 2004; Fiksen et al., 2007; Staaterman et al., 2012; Wolanski and Kingsford, 2014). Several reviews also stressed the importance of considering *realistic* larval fish behavior in biophysical models (Leis, 2007; Miller, 2007; North et al., 2009; Catalán et al., 2013; Staaterman and Paris, 2014). The reviews' main recommendations are to implement empirically observed behaviors, measured on the species that is modeled (not on a related one, unless if they do not differ), and to include behavior changes that occur throughout ontogeny. Given this amount of evidence and recommendations, today, it would clearly be wrong to apply the "simplifying assumption" (sensu Leis, 2006) and consider fish larvae as passively drifting particles advected by the currents.

However, mainly because of the historical lack of data on larval fish behavior, most models made this assumption, or only considered simple vertical migrations behavior (e.g., Johnson et al., 2013; Nanninga et al., 2015). This is particularly true in the Mediterranean Sea. For example, Di Franco et al. (2012) and Koeck et al. (2015) did not include any behavior in their biophysical model. Yet, they used these models, among other approaches, to test the maximum potential dispersal of *Epinephelus marginatus* (Lowe, 1834; dusky grouper) larvae (Koeck et al., 2015) or of white seabream *Diplodus sargus* L. (Di Franco et al., 2012; Pujolar et al., 2013) larvae from a network of MPAs. The youngest larval stages may indeed be considered as passive and, providing the physical model is adequate, the initial export of propagules should therefore be correctly represented (Leis, 2007). However, this is not true for later stages and omitting larval behavior might induce large errors in the estimation of connectivity among MPAs, especially a species with such a long pelagic larval duration (PLD) (about 25 days; Macpherson and Raventos, 2006).

To overcome the lack of behavioral data for this species, Andrello et al. (2013, 2015) ran two sets of simulations, the main one with passively drifting particles and a second one with diel vertical migrations between 0.2 and 50 m, throughout ontogeny. They found the connection distances to be >100 km on average and concluded that diel vertical migration had little influence on the connectivity patterns.

Some models focused on the Mediterranean Sea did implement directional swimming. Basterretxea et al. (2012) first assessed the connectivity in a network of MPA and found that passive retention reaches >30% within 10 km of the seeding MPA. Then, Basterretxea et al. (2013) tested the influence of swimming at 5 cm s^{-1} toward the coast, while advection transported the larvae offshore. It resulted in slightly higher retention rates (41%), yet still of the same order of magnitude. Faillettaz et al. (2017) implemented shoreward swimming at various speeds, based on empirical data, in a model of the competency period. In that case, the model suggested that swimming abilities of just few cm s^{-1}, over only 4 days at the end of the pelagic phase, can strongly influence the rate of recruitment.

The contrast among these results, both among studies in the Mediterranean Sea and with studies elsewhere (which, almost systematically concluded that behavior strongly influenced dispersal patterns) makes it difficult to reach a conclusion. In addition, the only models that explicitly studied connectivity within the network of Mediterranean MPAs did not include swimming behavior. The present work is a case-study for the inclusion of larval behavior when assessing connectivity within a network of MPAs, with an application to the dispersal of Sparidae (sea breams) larvae in the Ligurian Sea (N-W Mediterranean Sea). We track virtual larvae throughout their pelagic phase and compare a passive scenario with an active one, in which we implement an oriented swimming behavior based on all data available for the species considered.

METHODS

Study Area

This study was conducted in the Ligurian Sea, in the Northwestern Mediterranean Sea. In the region, the main hydrological structure is the Liguro-Provençal current, positioned on average 28 km from the shore (**Figure 1**), between the surface and 150–200 m depth, 25 km wide and flowing at 25–35 cm s^{-1} toward the south-west (Béthoux and Prieur, 1983; Stemmann et al., 2008). The current is present throughout the year and creates a marked hydrological front that may act as a barrier to offshore dispersal of coastal organisms (Pedrotti and Fenaux, 1992) comparable to other Mediterranean fronts (Galarza et al., 2009).

We focused on three MPAs located in the northern Ligurian Sea, where most behavioral data available for the species of this region has been collected (in and around the Bay of Villefranche-sur-Mer; 43.69°N, 7.31°E; **Figure 1**): The northernmost is the Larvotto MPA (Monaco, 43.7°N, 7.4°E; **Figure 1**) with 0.349 km^2 closed to fishing activities since 1976. The second MPA is located in Cap Roux (France, 43.5°N, 6.9°E; **Figure 1**) and comprises an area of 4.45 km^2 closed to fishing established in 2003. The third is the National Park of Port-Cros, a 29 km^2 MPA established in 1963, in and around the islands of Port-Cros and Porquerolles (France, 6.4°E, 42.9°N).

Hydrodynamic and Lagrangian Models

Ocean current fields were provided by MARS3DMed (Ifremer). This model is described in detail in Lazure and Dumas (2008) and has been validated with observations (Pairaud et al., 2011). Current fields are available every 3 h, on a 1/64° grid (ca. 1.2 km), over 60 sigma layers, and cover the most of the NW Mediterranean Sea, from 0° to 15°E and 39.5° to 44.5°N. We used currents from June 1st to August 29th 2014, the main settlement period for larval fishes in the region (Faillettaz, 2015) and when behavioral data on swimming speed and orientation has been collected (Faillettaz et al., 2015, 2017).

Virtual larvae were simulated using the open-source Connectivity Modeling System (CMS; Paris et al., 2013). At each time-step, this Lagrangian model couples deterministic physical variables from a hydrodynamic model with probabilistic, individual-based biological characteristics such as spawning (location and date), mortality and vertical migration (diel and ontogenic). Of particular interest here, the CMS is the only full-fledged Lagrangian model that also comprises a biased and correlated random walk sub-model that can be used to simulate the oriented swimming behavior of virtual larvae (Staaterman et al., 2012). Swimming speed is set in cm s^{-1}. The direction of orientation can be set to follow a bearing or a target. The precision of orientation is set by the k parameter of a Von Mises distribution (the circular equivalent of a Normal distribution), which ranges from 0 (no orientation) to 5 (high accuracy; Codling et al., 2004). Settlement zones are defined as polygons, drawn by adding a spatial buffer around actual settlement habitat. When a competent larva enters a polygon, it is considered as settled and stops moving, assuming that it will successfully reach the closest favorable settlement habitat within the polygon.

Horizontal diffusivity was set to 10^5 cm^2 s^{-1} based on diffusion diagrams from Okubo (1971) and the time-step was set to 300 s (1/36th of the hydrodynamic model output time-step). Maximum current speeds were around 0.5 m s^{-1}, which resulted in a maximum passive displacement of 150 m within one time step, well below the 1.2 km grid size, hence avoiding numerical issues during trajectory computation.

Simulations Scenarios

Modeled Species

We focused on two groups of sea bream species, identified as "small Sparidae" (i.e., 9–11 mm in standard length) and "large Sparidae" (i.e., 14–16 mm in standard length), because their morphology and behavioral abilities were found to be similar within group but different between groups (Faillettaz et al., 2017). Small Sparidae comprise, at least, *Boops boops* Linnaeus, 1758, *Oblada melanura* L., *Spicara smaris* L. and *Diplodus annularis* L. Large Sparidae comprise species such as *Dentex dentex* L., *Pagellus acarne* Risso, 1827, *Pagrus pagrus* L. and *Spondyliosoma cantharus* L. Larvae of small Sparidae are slenderer, less pigmented, and seemingly less developed at settlement than those in the large Sparidae group. Small Sparidae also swim slower than large Sparidae (Ucrit = 11.1 vs. 19.2 cm s^{-1}; Faillettaz et al., 2017) and their pelagic larval duration is shorter (14–18 d on average vs. 30–38 d; Raventós and Macpherson, 2001; Macpherson and Raventos, 2006).

Particle Seeding

In each of the three MPA (Larvotto, Cap Roux, and Port-Cros), 1500 virtual larvae were seeded at 1 and 15 m depths, twice per day, at 10:00 p.m. and 2:00 a.m., every day from June 1st to 15th and from July 1st to 15th, to match the patterns of larval supply measured in the Bay of Villefranche-sur-Mer: presence of Sparidae between the last and the first quarters of the moon, in June and July 2014 (Faillettaz, 2015). In total, 540,000 larvae were tracked per simulation.

Biological Parameters

The species of the two modeled groups settle in relatively similar coastal habitats (i.e., in seagrass and rocky or soft bottoms; Nelson et al., 2016) and the geomorphology of the study region is homogeneous, with rocky capes and sheltered bays every few kilometers from Genova (Italy) to Toulon (France) and in Corsica. The whole coastline was therefore assumed to be a potential settlement habitat and divided in ∼8 km^2 polygons (∼4 km of coastline × 2 km offshore, yielding 265 polygons). Given the scale of the study (∼500 km of coastline) relative to

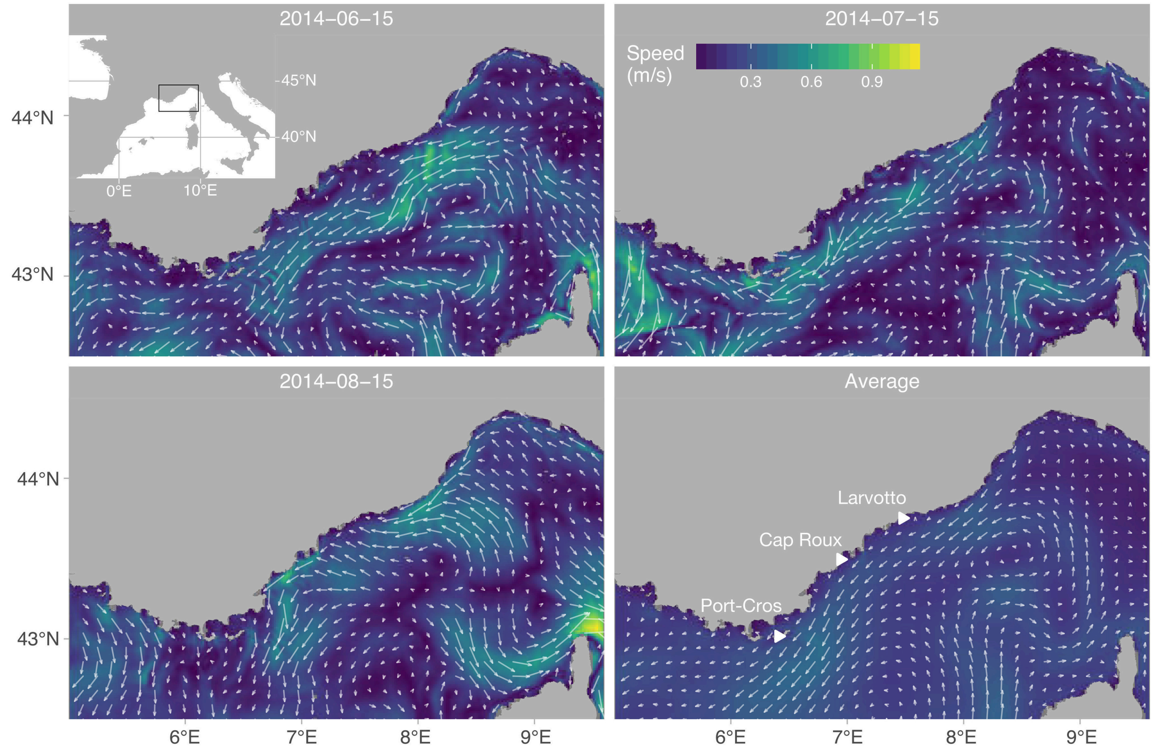

FIGURE 1 | Map of the study region, with simulated current field snapshots at 5 m depth and averaged over the study period. Flow vectors are overlaid on top of a linearly interpolated map of average current intensity. The typical strong jet along the northern coast is highlighted, as well as two stable mesoscale eddies: a well defined cyclone (counterclockwise) centered on 8.5°W, 43.5°N and a weaker anticyclone below. Triangles indicate the three MPAs from where virtual larvae were released.

the size of the settlement polygons (4 km of coastline) and of the grid (1.2 km), the possible small deviations from this assumption of uniform habitat distribution would have little influence on the results. Furthermore, most of the region is characterized by a narrow continental shelf, with bottom depth >300 m within a kilometer from the coastline. The offshore expansion of coastal habitats, and of the coastal fish populations they support, is therefore limited to nearshore areas ($\leq$1 km). To avoid boundary issues in the interpolation scheme, we considered that virtual fish larvae could detect a coastal settlement habitat from as far as 2 km (1.5 grid point) from the shore and reach it. Such an assumption is common in Lagrangian models (Cowen et al., 2006; Wolanski and Kingsford, 2014) because settlement habitats and processes cannot be described at the appropriate scale given the coarseness of the models' grids ($\sim$1.2 km here).

Mediterranean larvae of Sparidae are mostly concentrated in the upper 10 m of the water column, with very limited to negligible diel vertical migration (Sabatés and Olivar, 1996). Larvae were therefore simulated on fixed, near-surface sigma levels.

Mortality would decrease the settlement rate but was not considered in the model because only constant mortality rates could have been implemented, which would not have altered the relative settlement rates predicted.

Two simulations were run for each of the two groups of Sparidae: one with passively drifting virtual larvae and the other with oriented swimming. For "passive" simulations, the only parameter that differed between Sparidae groups was the pelagic larval duration (PLD). To account for the flexibility in the competency phase, which can span up to several days in Mediterranean species of sea breams (Calò et al., 2016), small Sparidae were considered competent from 13 to 19 days and large ones from 28 to 38 days. Larvae that reached a settlement polygon within their competency period were considered as settled. Larvae that did not reach a polygon by the end of their PLD were considered as dead. For "active" simulations, swimming speed and orientation abilities were implemented based on empirical observations carried out within the simulated region and period, for the two groups of Sparidae considered (Faillettaz et al., 2015, 2017).

During the competency phase, swimming speed was set to half the critical speed measured by Faillettaz et al. (2017). This is an estimate for the *in situ* speed, a speed that accounts for feeding-related speed changes, is assumed to be sustainable over long periods of time, and is therefore a conservative estimate for the swimming abilities of wild larvae (Leis and Carson-Ewart, 1998; Leis and Clark, 2005; Leis and Fisher, 2006). The ontogeny of swimming abilities was based on observations for other temperate and tropical fish larvae (Fisher et al., 2000; Clark et al., 2005; Leis et al., 2007; Faria et al., 2009): swimming speed was negligible before flexion, after the flexion (8 days; Leis, 2010) it was set to 1 cm s^{-1} and then increased linearly to 6 cm s^{-1}

at 13 d for small Sparidae and to 10 cm s^{-1} at 28 d for large Sparidae.

Similarly, the orientation abilities of species belonging to the two groups of Sparidae were investigated in the same location and time of the year (Faillettaz et al., 2015). The vast majority of individuals (>85%) followed a cardinal bearing while in blue waters and most used the sun's azimuth as a compass, providing a potential mechanism for large-scale orientation in the open ocean. Shoreward swimming during the larval phase is a relatively simple behavior that the existence of such a compass would enable. By limiting the loss of individuals in the open sea at the end of the larval phase, it would systematically increase survival and should therefore be strongly selected for, given the intense mortality experienced by fish larvae (Houde, 2008). More complex behaviors, such as orientation corrected for the drift due to currents or exploiting current structures (eddies, shears, etc.), would be even more favorable, but the sensory mechanisms and cognitive requirements involved are still unexplored. To compute the plausible influence of directional swimming on advection trajectories based on the current state of knowledge, swimming was aimed at the coastal polygon closest to the larva at each time step (i.e., without course correction). Orientation precision was set higher for large Sparidae ($k = 4$) compared to small Sparidae ($k = 3.5$). The values of k were estimated by fitting Von Mises distributions to the orientation bearings recorded for the two groups in Faillettaz et al., 2015).

Data Analysis

For each simulation, the proportion of successful settlers was computed as the number of virtual larvae that reached a coastal polygon during their competency phase divided by 540,000 (the number of larvae released). The proportion of settlement per MPA was computed the same way but considering only larvae reaching MPA polygons, i.e., polygons within 3 km of an MPA, to account for the fact that the resolution of the hydrodynamic model (∼1.2 km) is not sufficient to describe local scale fluid dynamics.

The retention rate was defined as the number of larvae that were released from an MPA and settled in that same MPA's polygons, divided by the number of larvae released from that MPA. The self-recruitment rate was computed with the same numerator (number of particles that originated from and settled in the MPA) but divided by the total number of larvae that settled in the MPA, regardless their origin.

Dispersal kernels were computed as the probability density function of the great circle distance between the release MPA and the settlement location of successful settlers. The probability density function was estimated with a Gaussian smoothing kernel.

RESULTS

Most virtual larvae as advected outside the domain, although small Sparidae do not move as far from their release sites as large Sparidae (**Figure 2**), simply because their pelagic phase is shorter. The overall proportion of successful settlers was strongly increased by the inclusion of larval behavior, for both groups of Sparidae (**Figure 3**): 16.3% (passive) vs. 28.4% (active) for small Sparidae and 1.2% (passive) vs. 10.2% (active) for large Sparidae. It was also always higher for small Sparidae compared to large Sparidae. However, the relative change induced by the inclusion of behavior was larger for large Sparidae: × 1.7 for small Sparidae vs. × 8.7 for large ones.

The proportion of virtual larvae that settled within any of the three MPA was low, with a maximum of 1.18% for passive small Sparidae in Larvotto and a minimum of 0.01% for passive large Sparidae in Port-Cros (**Figure 4**). For small Sparidae, the inclusion of larval behavior decreased the proportion of settlement by about half in Larvotto and Cap Roux, while it tripled it in Port-Cros. For large Sparidae, active swimming yielded at least a five-fold increase in the proportion of settlement in any of the three MPAs (**Figure 4**).

Since the overall recruitment rates in MPAs were low, retention rates within each MPA were also low (<1%; **Figure 5**). However, including larval behavior markedly increased retention, except for small Sparidae in Cap Roux. Unsurprisingly, this higher retention of active larvae translated into higher self-recruitment rates, while the lower retention of small Sparidae in Cap Roux translated into a lower self-recruitment rate. However, an interesting pattern occurs for large Sparidae in Larvotto: active swimming yields higher retention but lower self-recruitment proportions. This means that the settlement of larvae from both Larvotto itself and the other MPAs increased when larvae were swimming, but the import of larvae from Cap Roux and Port-Cros increased more than the retention from Larvotto.

Dispersal kernels show relatively few differences between simulations (**Figure 6**), with a consistent peak in larval supply to coastal habitat centered around 180–200 km away from the release MPA. Sill, passive small Sparidae displayed the lowest mean dispersal distance (141.1 ± 64.2 km; median = 146.2 km), followed by active small Sparidae (147.2 ± 71.4; median = 157.1 km), then active large Sparidae (149.5 ± 76.3; median = 167.2 km), and finally passive large Sparidae dispersed furthest (156.9 ± 67.2 km; median = 176.1 km). All kernels were statistically different from each other (Kolmogorov-Smirnoff tests, all $D = [0.04–0.13]$, all $p < 0.001$). In the passive case, the shorter distances (to the left of the peak) are observed more often for small Sparidae compared to large ones. Conversely, larger dispersal distances are more often reached by large Sparidae than by small ones. The inclusion of larval behavior slightly increased larval supply within the closest 100 km for large Sparidae and *circa* 230 km for small Sparidae (**Figure 6**).

Beyond those differences in terms of dispersal kernels, including larval behavior substantially increased the number and intensity of connections throughout the Ligurian Sea (**Figure 7**). It is noteworthy that the three MPAs have the potential to export larvae of large Sparidae throughout the region. Fewer connections occur for small Sparidae compared to large Sparidae, but the intensity of those connections is generally higher, echoing the overall higher proportion of settlement of small Sparidae. In the passive simulations, the eastern region (Italian coast) received fewer larvae from the three MPAs considered than the rest of

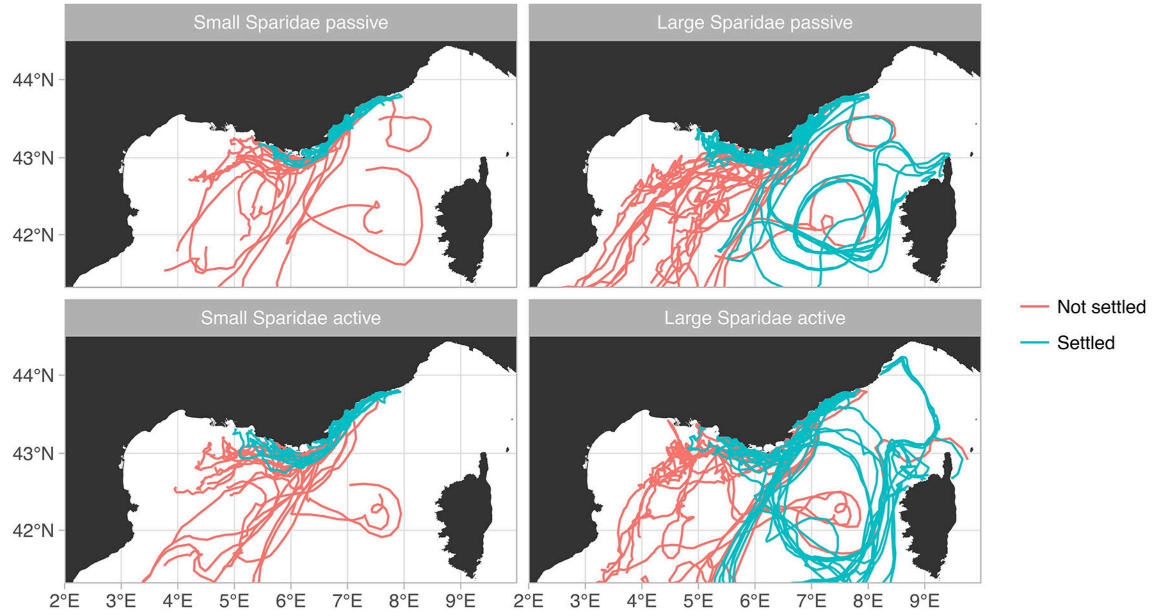

FIGURE 2 | Examples of trajectories from each simulation.

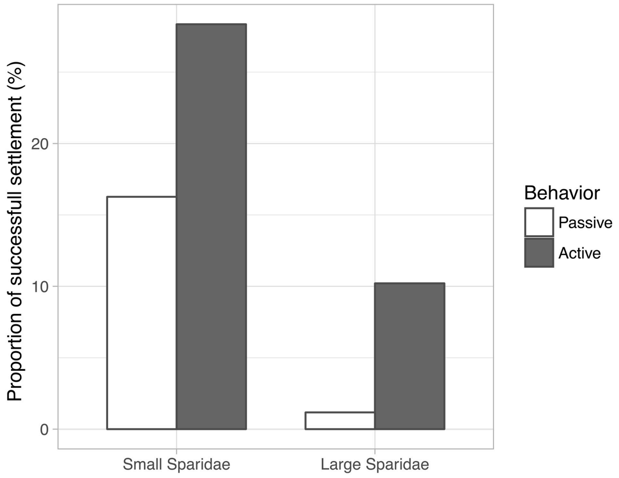

FIGURE 3 | Proportion of virtual larvae that successfully reached a coastal habitat during their competency phase.

the domain (**Figure 7**). This pattern that was not as pronounced when behavior was added.

DISCUSSION

Generalization of the Present Results

We used a relatively simple example, based on a network of three French MPAs located in the Ligurian Sea, a part of the northwestern Mediterranean Sea, to reveal the potential differences in dispersal outcome that may be expected when accounting for oriented swimming by fish larvae.

We observed an increase in the overall proportion of settlement (**Figure 3**). This is intuitive since virtual larvae were parameterized to swim toward coastal habitats. All other things being equal, one would expect an increase in settlement rate proportional to the swimming speed (Faillettaz et al., 2017). More surprising however, is the lower proportion of large Sparidae that reached coastal habitats compared to small Sparidae, while they swam about twice as fast (10 cm s^{-1} at settlement vs. 6 cm s^{-1} for small Sparidae). The settlement rate of large Sparidae was even smaller compared to that of small Sparidae when larvae drifted passively. This difference is therefore probably attributable to the difference in PLD (13–19 d for small Sparidae vs. 29–38 d for large ones). Indeed, virtual larvae with a longer PLD may drift further away from their hatching site, which reduces the probability of reaching a coastal settlement habitat before the end of their competency phase. This highlights the foremost importance of the PLD in controlling larval supply rates, as suggested by several studies (e.g., O'Connor et al., 2007; Andrello et al., 2013).

Species with short PLDs, like small Sparidae, should therefore not drift as far as species with long PLDs, such as large Sparidae. In passive simulations, this is confirmed by the shape of the dispersal kernels, which highlight more short dispersal distances for small Sparidae (**Figure 6**), and the higher retention rates of small Sparidae (**Figure 5**). However, including behavior completely changed these retention patterns, indicating that retention is mostly determined by larval behavior rather than advection.

The fact that even the fastest-swimming larvae settled in relatively low numbers suggest that their swimming abilities

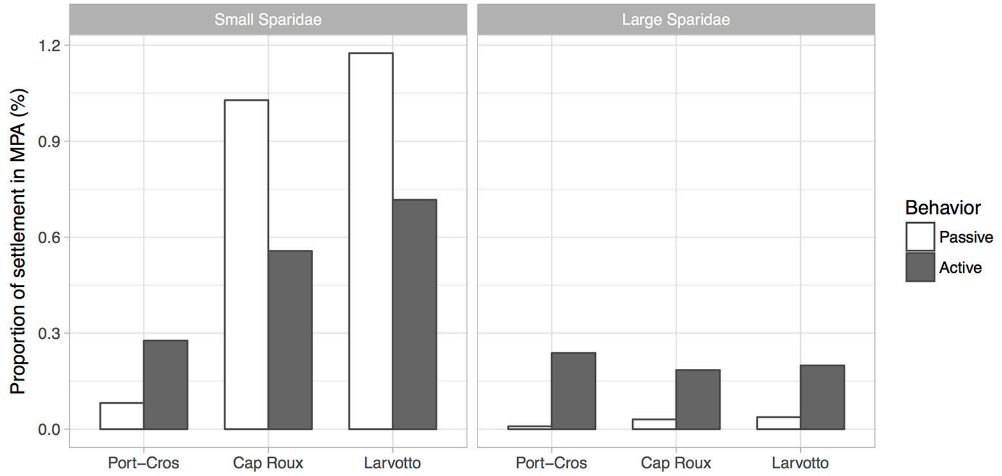

FIGURE 4 | Proportion of virtual larvae that successfully reached a coastal habitat within an MPA during their competency phase.

are not sufficient to fully counteract the advection by oceans currents, when they drift too far offshore. Yet, considering their behavior still lead to a 9-fold increase in the overall proportion of settlement, for large Sparidae. This suggests that the relatively simple swimming behavior implemented in this model would be a much more favorable strategy in the face of natural selection, than randomly drifting with the flow.

In terms of connectivity patterns, active swimming increased the number and intensity of connections throughout the region, and in particular toward Corsica and the Italian coast (**Figure 7**). The lower intensity of connections to these regions in the passive case can be explained by the persistent Ligurian current, which transports particles mostly westward, at a fast pace, limiting eastward and southward connections. Our results suggest that, in this configuration of the coastline, larval behavior would favor connectivity at regional scale, in all directions. Accounting only for the general flow direction may thus not properly represent the main patterns of spillover.

We can compare the dispersal patterns of passively drifting larvae simulated here to the results of Andrello et al. (2013), who modeled the dispersal of *Epinephelus marginatus* (dusky grouper) among MPAs located throughout the Mediterranean Sea. They included the MPA of Port-Cros and set the PLD of *E. marginatus* to 30 d, which is in the range of PLDs considered for the large Sparidae we modeled (29–38 d). In the study by Andrello et al., self-recruitment accounted for most of the settlement, across all MPAs, but the MPA of Port-Cros was one of the six MPAs (over 99) that presented zero self-recruitment. Based on our passive simulation, we might also have concluded that Port-Cros may acts exclusively as a source MPA (**Figure 5**), but we actually showed that it becomes the MPA with the highest potential of self-recruitment rate when larval behavior is added, hence reversing the initial conclusion.

In summary, we found that including larval behavior in the model has (i) increased the overall proportion of successful settlers, (ii) enhanced self-recruitment within the MPAs, but also (iii) increased the intensity and (iv) widened the potential export of propagules from the MPAs. In line with previous modeling studies that focused on behavior (e.g., Paris et al., 2007; Staaterman et al., 2012; Wolanski and Kingsford, 2014), our results show the importance of exploring the potential effect of larval behavior when predicting connectivity patterns. Given the diversity of patterns detected here, which echoes that of other studies (e.g., Paris et al., 2007), the influence of larval behavior should definitely not be generalized as solely reducing the scales of connectivity, as it has been regularly suggested (Sponaugle et al., 2002; Andrello et al., 2013).

Toward More Accurate Connectivity Models in the Mediterranean Sea

Biophysical dispersal models have become a common tool for management and planning purposes. Yet, most still omit larval behavior, while this study adds to the evidence that larvae swimming at even just a few cm s^{-1} may substantially influence the outcomes of the pelagic phase (Werner et al., 1993; Leis, 2007; Vikebø et al., 2007; Staaterman et al., 2012; Wolanski and Kingsford, 2014; Faillettaz et al., 2017). But, to implement larval behaviors in a meaningful way, empirical data describing them is necessary.

Diel vertical migration behavior is well documented in fish larvae, including in the Mediterranean (Olivar and Sabatés, 1997; Sabates, 2004; Sabatés et al., 2010). Mediterranean coastal fish assemblages are dominated by perciformes and all perciformes larvae studied so far have been shown to swim at high, sustained speeds (Leis, 2006). In addition, it seems that their morphology could provide information on their swimming abilities in the absence of data on the species of interest (Fisher and Hogan, 2007; Faillettaz et al., 2017). Finally, swimming speeds achievable early during ontogeny can be somewhat inferred from swimming abilities during the installation phase, which is easier to study (Leis, 2010).

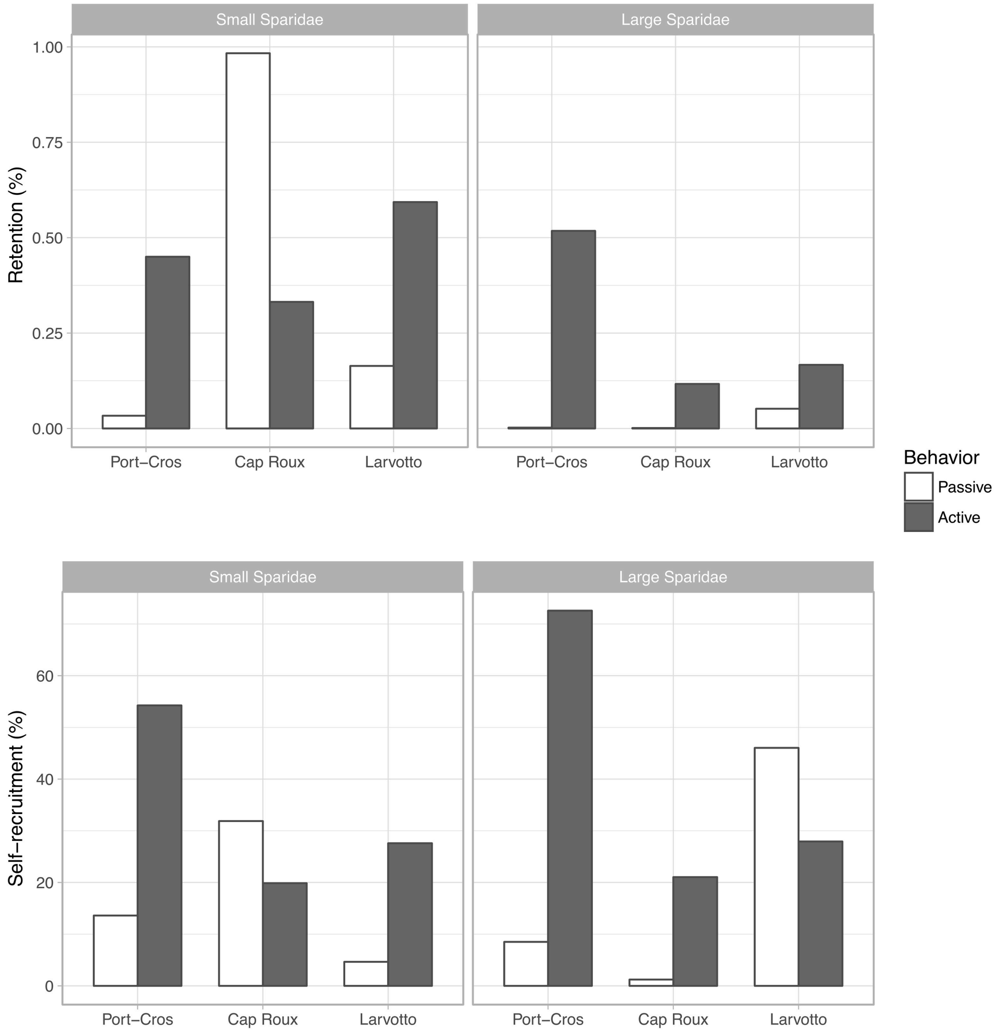

FIGURE 5 | Retention rate (i.e., number of virtual larvae that originated from and settled in a given MPA divided by the number of virtual larvae that were released from that MPA) and self-recruitment rate (i.e., same as self-retention but divided by the number of virtual larvae that successfully settled in the MPA) for each release MPA and group of Sparidae.

Information on the swimming abilities of Mediterranean species is scarce (see Faillettaz et al., 2017 for a complete account) but estimations of their orientation abilities are even more so (Faillettaz et al., 2015 is the only study so far), and this is actually true all over the world (Leis, 2006). Yet, oriented swimming is likely to have a major impact on dispersal, especially if it occurs early in the larval phase (Staaterman et al., 2012).

Additional data on swimming abilities of young larvae and orientation abilities throughout ontogeny would therefore be the most critical to collect currently. When no data is available, the bias associated with their absence could be estimated by comparing dispersal patterns obtained from passive simulations and from simulations of caricatured behaviors (e.g., swimming at high speed and perfectly oriented), as part of a sensitivity study. North et al. (2009) provide suggestions for the implementation of such sensitivity approaches and Basterretxea et al. (2013) is an example of such a study in the Mediterranean.

Another essential criterion for the correct use of Lagrangian models is whether the spatial resolution of the underlying oceanographic model and the time step for the integration of the Lagrangian trajectories are adapted to the questions asked. In the present study, the grid of the hydrodynamic model (∼1.2 km) could not resolve coastal patterns. Therefore, we did not attempt to represent them in the biological model and considered that larvae were able to reach the coast when they arrived within two kilometers of it (i.e., ∼1.5 grid points). Overall, we interpret the predicted patterns of connectivity at scales of tens to hundreds of kilometers, for which the resolution of 1.2 km is not limiting. In contrast, to answer similar questions (regional connectivity and rates of larval retention), other studies used much lower resolutions (e.g., >12 km; Andrello et al.,

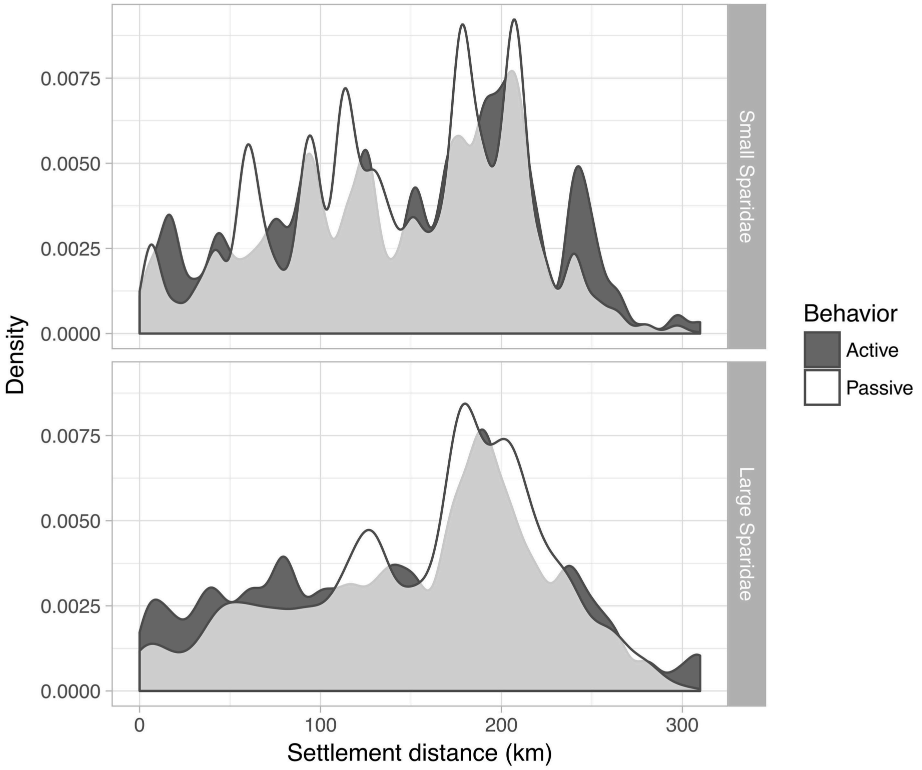

FIGURE 6 | Dispersal kernels for the two groups of Sparidae and the two simulation configurations, i.e., kernel density smoothing of distances from the release site to the settlement site.

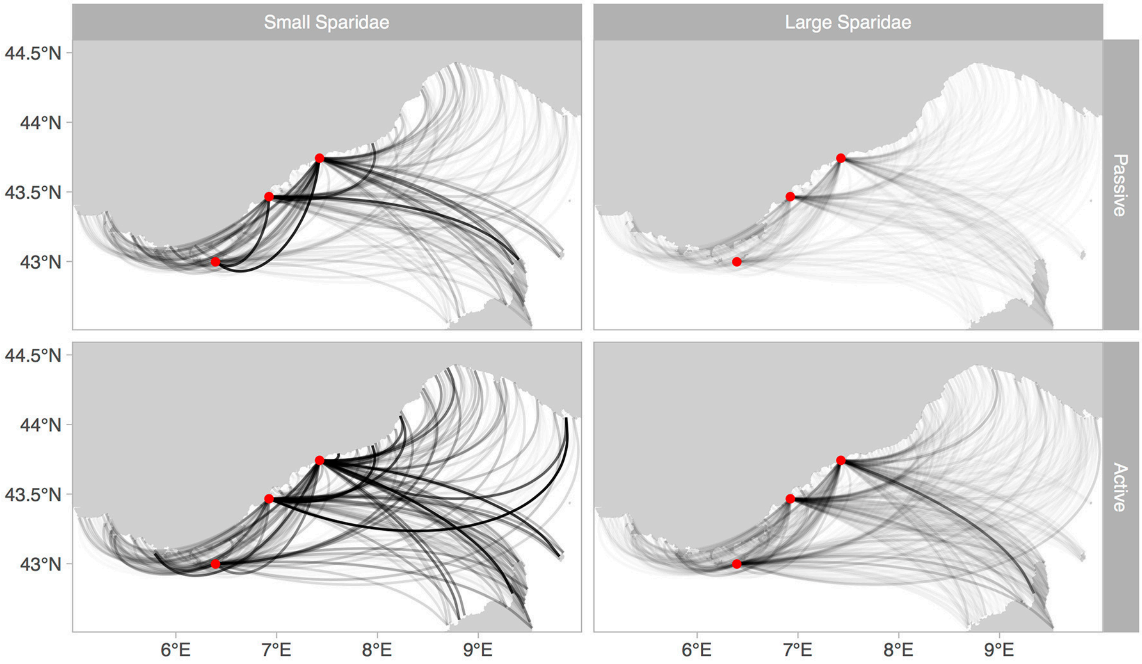

FIGURE 7 | Connectivity patterns throughout the Ligurian Sea, from the three release MPA (red dots). Lines represent connections, not dispersal trajectories. Their intensity is proportional to the intensity of the connections.

2013, 2015) or integration time steps allowing larvae to cross more than one grid cell in a single step (Basterretxea et al., 2013). Such use of unsuitable configurations could skew the dispersal patterns obtained (North et al., 2009). To avoid these biases and better address near-shore, small-scale circulation processes, which are essential for egg dispersal and, perhaps, the installation of late larval stages, hydrodynamic models with higher resolution, especially near the coasts, are essential. Near-shore environment (e.g., bathymetry, habitat, etc.) may also affect larval fish sensitivity to coastal cues and considering these processes may help in further improving biophysical models.

Patterns of dispersal are also strongly influenced by the precise location and date of spawning (e.g., Guizien et al., 2012). However, in the North-Western Mediterranean Sea, the spawning areas of Sparidae, for example, are poorly known. We had to assume that they spawned along the coast, where they live. Their settlement and preferential recruitment habitats are better documented but often very restricted spatially (Vigliola et al., 1998; Cheminee et al., 2011). For example, around Marseille (France), the settlement habitat of the genus *Diplodus* could be limited to as little as 9% of the coastline. Nevertheless, this level of detail in the definition of settlement locations is not usually represented in dispersal models because accurate habitat mapping at the scale relevant to the models is not available (but see Holstein et al., 2014 for an example in the Caribbean Sea). Here, we again had to assume that suitable habitat, although possibly scarce, was uniformly distributed along the coast. Mapping of coastal habitats is currently being conducted in the Ligurian Sea (Meidinger et al., 2013) and may allow to refine future connectivity models in the region.

Finally, the results presented in this study show that the success of the pelagic larval phase is governed by both oceanographic processes and suite of biological characteristics (swimming speed, orientation accuracy, etc.). However, the unitary effect of each behavior on larval dispersal has rarely been explicitly evaluated (Werner et al., 1993; Paris et al., 2007 are two, rare, examples). It would therefore be interesting to compare a model simulating all observed larval behaviors with degraded versions in which behaviors are removed one by one, in order to quantify their respective effects and determine the importance of including them in connectivity models. Such a sensitivity analysis could effectively guide the collection of empirical data on the behavior of fish larvae in the future and, ultimately, improve the reliability of biophysical models. It would be particularly relevant in the context of the necessary improvement of the network of marine protected areas required by the European Union. Indeed, describing connectivity through the simulated dispersal of propagules is becoming a usual tool for the management and conservation of marine resources, particularly for the establishment of new protected (or urbanized) areas. Nevertheless, such approach may lead to the wrong conclusions if the biological components are not accurately parameterized because empirical data is lacking.

AUTHOR CONTRIBUTIONS

RF, CP, and J-OI designed the modeling experiment. RF and J-OI run the simulations. RF analyzed the data and wrote the manuscript. CP and J-OI revised the manuscript.

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Nearshore Larval Retention and Cross-Shelf Migration of Benthic Crustaceans at an Upwelling Center

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Planktonic larvae are thought to be very susceptible to offshore advection in upwelling regimes, increasing dispersal and decreasing recruitment. However, larvae of 42 species of nearshore benthic crustaceans primarily developed on the inner shelf at locations both in (98.5%) and away (99.8%) from a perennial upwelling center in the upwelling season of a recruitment-limited region characterized by persistent, strong, upwelling. During three cross-shelf cruises conducted at each location, larvae of 21 species remained on the inner shelf at both sites by occurring beneath seaward-flowing surface currents while larvae of other species migrated to midshelf (four species) or offshore (14 species) by initially developing near the surface. Postlarvae apparently returned to shore either deep in landward-flowing upwelled water or near the surface where behavior allows them to be transported shoreward by internal waves, diel wind cycles or wind relaxation events. Thus, recruitment limitation in upwelling regimes does not appear to be caused by larval mortality from offshore transport, requiring new research directions to advance our understanding of population dynamics, structure and connectivity.

Keywords: larval transport, behavior, population connectivity, recruitment limitation, upwelling

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INTRODUCTION

Variation in larval recruitment often determines population and community dynamics in the sea. Both larval dispersal and mortality have been challenging to measure rendering estimates of population connectivity uncertain. Moreover, the ability of larvae to regulate transport could have a large impact on dispersal and population connectivity and has been debated for decades. We recently determined that larvae occurred close to shore in persistent, strong upwelling on the Pacific Coast of the USA—rather than lost offshore as was widely expected (Morgan et al., 2009b,c, 2011; Morgan and Fisher, 2010; Fisher et al., 2014; Hameed et al., 2018)—and that larval mortality in the nearshore retention zone was much lower than previous estimates of larval mortality anywhere (White et al., 2014). We then demonstrated that larval behaviors enabling larvae to remain close to shore throughout development also enable them to settle near natal populations (Drake et al., 2013; Hameed et al., 2016). We now investigate whether larvae also completed larval development close to shore at one of the strongest upwelling centers further reducing the scale of population connectivity.

On the west coasts of continents, strong wind and Coriolis generate seaward-flowing surface currents (Ekman transport) dropping sea level along the coast while upwelling deep, cold water (Hickey, 1998). It has been suggested that larvae of nearshore species are lost to offshore transport by persistent, strong upwelling conditions (Parrish et al., 1981; Roughgarden et al., 1988; Menge and Menge, 2013), especially at the apex of headlands and immediately equatorward, where wind stress is most intense (Winant et al., 1988; Koracin et al., 2004) as well as at headlands where alongshore flow separates forming an offshore-directed jet (Barth et al., 2000; Kaplan and Largier, 2006). Meanwhile, flow may curve shoreward on the downstream of headlands resulting in onshore flow (Shannon et al., 1981; Halle and Largier, 2011) or forming a separation eddy where larvae may be accumulated (Wing et al., 1995, 1998; Graham and Largier, 1997; Roughan et al., 2005; Mace and Morgan, 2006a; Morgan et al., 2011; Ryan et al., 2014). Thus, larvae are widely expected to be most prone to offshore transport in upwelling centers and immediately downstream of headlands, limiting recruitment and enhancing dispersal away from this source, whereas farther downstream of headlands, they may be entrained in an eddy or transported onshore increasing recruitment and reducing dispersal away from this source.

Larval behavior may reduce transport at headlands and upwelling centers just as it does elsewhere along the coast. The characteristic vertical circulation in wind-driven upwelling areas enables invertebrate larvae and other zooplankters to reduce transport by regulating depth in vertically sheared currents (reviewed by Peterson, 1998; Morgan, 2014), as they do in other places where vertical shear occurs for different reasons (Epifanio and Garvine, 2001; Queiroga and Blanton, 2005; Morgan, 2006, in press; Epifanio and Cohen, 2016). Most species of larvae and copepods in upwelling regimes complete development close to shore within a coastal boundary layer, where Ekman transport is weak and alongshore currents are slow (Peterson et al., 1979; Morgan et al., 2009a; Shanks and Shearman, 2009; Morgan and Fisher, 2010; Nickols et al., 2013; Fisher et al., 2014; Hameed et al., 2018). They remain below a shallow Ekman layer or undertake diel vertical migrations, ascending near the surface to forage at night when offshore flow slows (Peterson et al., 1979; Peterson, 1998; Batchelder et al., 2002; dos Santos et al., 2008; Morgan et al., 2009a; Shanks and Shearman, 2009; Morgan and Fisher, 2010; Miller and Morgan, 2013). By avoiding upward transport into the seaward-flowing surface layer, they are subject to onshore flow and experience a flux convergence at the coast (Genin et al., 2005; Shanks and Brink, 2005). Different species are transported away from shore by occurring in the Ekman layer early in development and toward shore deep late in development, known as an ontogenetic vertical migration (OVM; Peterson et al., 1979; Grantham, 1997; Peterson, 1998; Mace and Morgan, 2006b; Papastephanou et al., 2006; Tapia and Pineda, 2007; Morgan et al., 2009a,b; Morgan and Fisher, 2010; Morgan, 2014). In some places or seasons, larvae late in development rise near the surface, known as a reverse ontogenetic vertical migration (ROVM), where behavior can allow internal waves, diel wind cycles or wind relaxations to transport them toward shore (Hobbs et al., 1991; Shanks, 1995a; Pineda, 1999; Poulin et al., 2002; Marta-Almeida et al., 2006; Morgan et al., 2009a; Morgan and Fisher, 2010).

We tested whether larval behavior effectively regulates transport at upwelling centers, as elsewhere, or whether it is overwhelmed by the intensity of wind forcing and currents. We compared cross-shelf and depth distributions of larvae of inshore benthic crustaceans along two transects near one of the strongest upwelling centers on the west coast of North America during the peak upwelling season. If larval behavior is overwhelmed, then (1) larvae should occur farther offshore at the upwelling center or (2) interspecific differences in larval behavior should render weak species more prone to offshore transport than others. If larval behavior effectively regulates larval transport, then cross-shore transport should be similar among species along the coast and to previous years. We also sampled beyond the shelf break to determine how many species are observed far offshore and potentially transported to the open ocean.

MATERIALS AND METHODS

Study System

We conducted the study within the perennial upwelling center of Point Arena in northern California (**Figure 1**), which is the windiest region along the Pacific Coast of North America (Koracin et al., 2004; Dorman et al., 2005). Prevailing northwesterly winds last for weeks in the spring-summer upwelling season, and near-surface waters (<50 m) flow equatorward and seaward (Hickey, 1998; Roughan et al., 2006). Shallow depths and coastline topography slow flow <10 km from shore (Lentz and Chapman, 1989; Largier et al., 1993; Kaplan et al., 2005; Kirincich et al., 2005; Nickols et al., 2012). This coastal boundary layer widens south of Bodega Bay where flows impinge on the upstream shores of Point Reyes (Robart, 2013) as equatorward flow is deflected offshore, separating from the apex of Point Reyes (Kaplan and Largier, 2006; Vander Woude et al., 2006). Upwelled water and plankton are entrained in an upwelling shadow in the lee of Point Reyes until winds weaken and alongshore flow reverses, transporting larvae poleward and onshore in less than a day (Wing et al., 2003; Roughan et al., 2006; Vander Woude et al., 2006; Morgan et al., 2011, 2012). This occurs about every 4 to 10 days (Send et al., 1987; Largier et al., 1993). Reversing flows result in little net alongshore transport (Largier et al., 1993; Kaplan et al., 2005).

Approach

We sampled stations across the shelf along transects off Bodega Head and in the upwelling center off Stewarts Point (**Figure 1**) toward the end of prolonged upwelling events when larvae are expected to be farther from shore, if simply advected by near-surface currents. We targeted three distinct upwelling events to sample different larval pools. We planned cruises using marine weather forecasts and offshore conditions at National Data Buoy Center 46013 (38° 13′ 30″ N, 123° 19′ 00″ W; http://www.ndbc.noaa.gov; **Figure 1**). We considered upwelling conditions to be northwesterly wind >5 m/s and water $<10°$C or decreasing. We surveyed vertical distributions of larvae at six stations along two cross-shelf transects on consecutive days on 28 and 29 May, 24 and 25 June, and 14 and 15 July 2009. The Bodega Head transect extended farther from shore as the continental shelf is wider. Stations at Bodega Head were located 1, 6, 11, 32, 42, and 63 km from shore at ∼20, 25, 80, 90, 100, and 120 m depth, respectively. Stations at Stewarts Point were located 1, 3, 10, 20, 30, and 49 km from shore at ∼20, 25, 80, 90, 100 and 120 m depth, respectively.

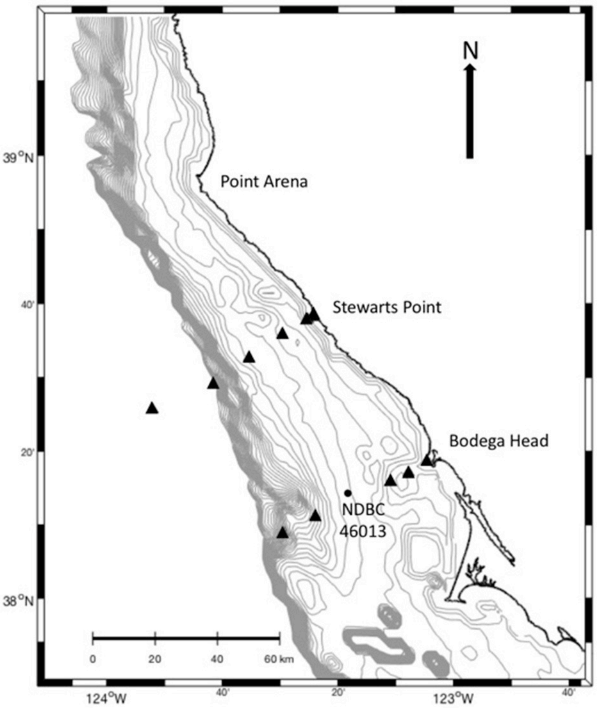

FIGURE 1 | Map of the study area depicting locations of stations along cross-shelf transects off Bodega Head and Stewarts Point in northern California. Location of NDBC buoy 46013 (•) is also shown.

We obtained wind velocity data from NDBC Buoy 46013 and calculated alongshore wind stress by converting it to true north and rotating it to 320° at an air density of 1.3 kg m^{-3} and a drag coefficient of 1.4×10^{-3} to place cruises in the context of upwelling conditions. We obtained water temperature and salinity from a Sea-Bird MicroCAT and chlorophyll-a fluoresence from a WET Labs EcoFluorometer, both at 4 m below the surface on moorings placed on the 15 m isobaths off Bodega Head and Stewarts Point from mid-May through July (**Figure 1**). In addition, temperature 1 m deep and 1 m above the seafloor was recorded with Onset Tidbit thermistors. We measured current using an acoustic Doppler current profiler (ADCP, 1,200 kHz; Teledyne RD Instruments, Poway, California, USA), which were bottom-mounted at moorings off Bodega Head and Stewarts Point at 30 m depth (**Figure 1**). We also mapped surface currents hourly across the study area using high-frequency (HF) radar.

We conducted three pairs of cruises along the two transects near the end of upwelling events, observed as periods of equatorward wind stress, cold water and low chl-a at the moorings off Bodega Head and Stewarts Point (**Figure 2**). Sampling on 28–29 May occurred at the onset of relaxation following a short upwelling event, with rising water temperature and chl-a and poleward flow (**Figure 3**). Sampling on 24–25 June occurred at the end of the strongest prolonged upwelling with temperatures still very low, even with the onset of relaxation on 25 June. Sampling on 14–15 July occurred at the end of a more moderate but prolonged upwelling event with winds and cold temperatures showing that relaxation had not yet started.

We collected plankton in daylight using an electronically tripped Tucker Trawl (0.5 or 1 m^2 mouth) with four nets (335-μm mesh) and temperature and depth sensors to take one sample above the thermocline and two samples below it. We sampled the

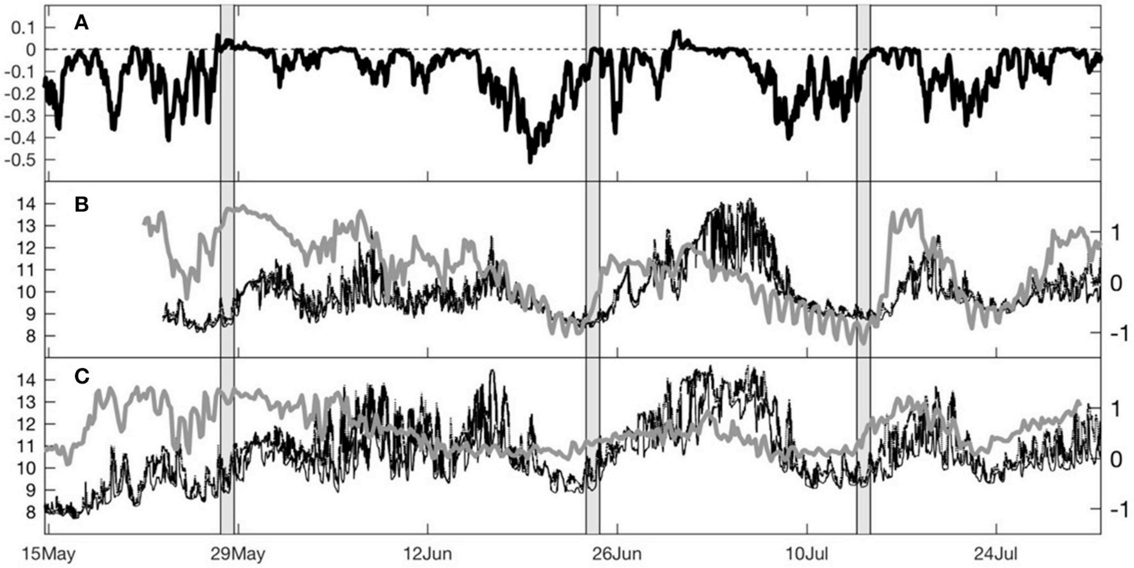

FIGURE 2 | Time series data from 15 May through 26 July 2009: **(A)** alongshore wind stress at NDBC buoy 46013, **(B)** Bodega Head temperature and chlorophyll-a fluorescence and **(C)** Stewarts Point temperature and chlorophyll-a fluorescence. Surface temperature shown as black line and bottom temperature as thin gray line, with chlorophyll-a fluorescence as thick gray line. Survey timing is indicated by vertical gray bars.

surface of the water column using a neuston net (0.5 m^2 mouth, 335-μm mesh). We profiled temperature and salinity with depth at the beginning and end of plankton tows using a conductivity, temperature and depth profiler (Sea-Bird 19-Plus).

We determined cross-shelf distributions for the 42 species of nearshore benthic crustaceans following our previous approach (Morgan et al., 2009b). Larval concentrations per m^2 standardized for the depth of the water column. We determined the cross-shelf and depth distributions of the 39 most abundant species over the six cruises with a nonparametric analysis of similarity (ANOSIM) and a hierarchical cluster analysis and ordination. After averaging depths at each station for the cruises, we determined that cross-shelf distributions of larvae were similar among dates (Bodega: ANOSIM $R = 0.054$, $p = 0.035$; Stewarts: ANOSIM $R = 0.045$, $p = 0.049$), so we averaged dates before conducting analyses on cross-shelf and depth distributions. We tested the resulting dendrogram for differences among groups with a similarity profile test (SIMPROF) and the percent contribution of each species and stage to significant clusters with (SIMPER) to classify cross-shelf and depth distributions for each combination of species and stage. Nonmetric Multidimensional Scaling (nMDS) revealed the separation of larval assemblages by distance from shore and depth. Contours of cross-shore and depth distributions of species by stage were plotted to evaluate whether depth regulation maintained different cross-shelf distributions. We combined species with similar depth distributions during development to simplify presentation and reported the mean depth center of mass (ZCM) and standard error for each species or group.

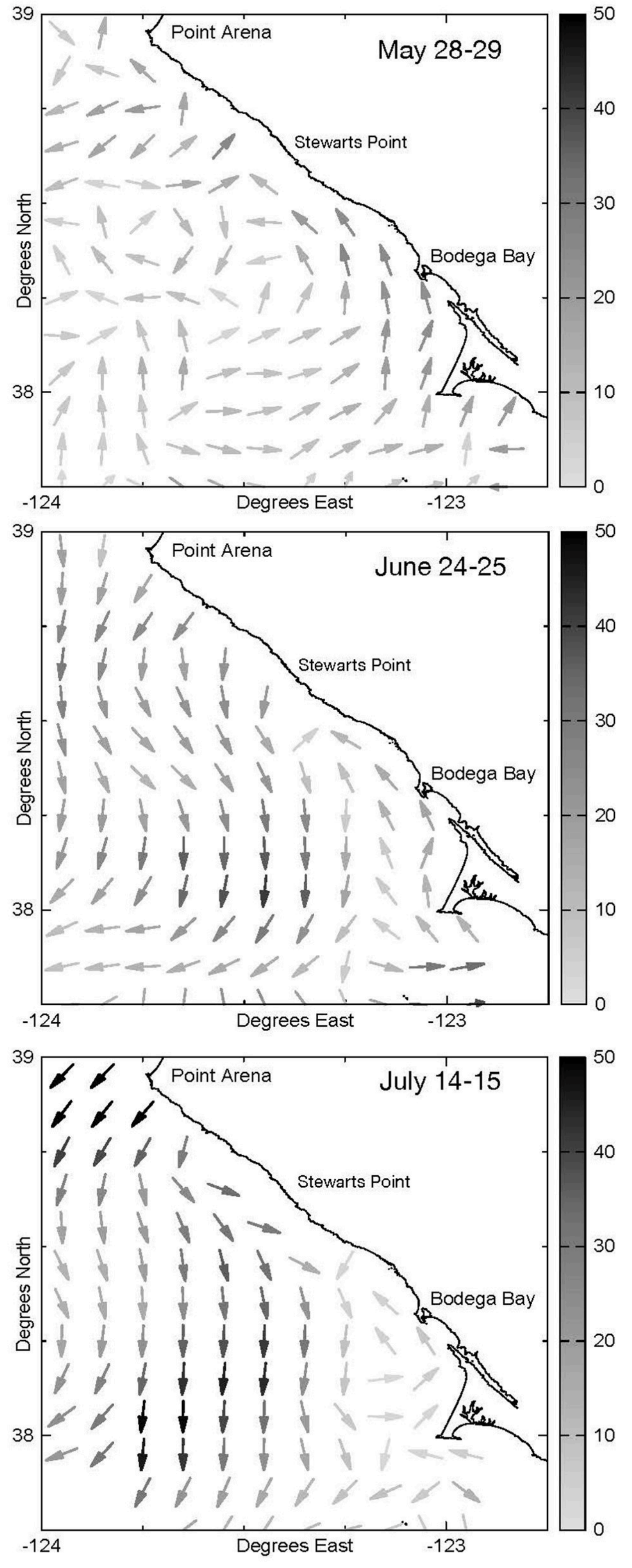

FIGURE 3 | Two-day mean surface current velocity recorded by high-frequency radar across the study region during cruises conducted on 28–29 May, 24–25 June, and 14–15 July 2009. Arrow orientation shows direction while darkness of shading represents speed (cm/s).

RESULTS

CTD profiles of temperature and chl-a revealed water column structure across the shelf along the two transects (**Figure 4**). On 28 and 29 May, a warm surface layer was observed, strongest nearshore and consistent with poleward flow–this layer was also characterized by high chl-a concentrations. On June 25 and 24 following a strong, prolonged upwelling event, cold waters shoaled nearshore with weak stratification off Stewarts Point on 24 June, but evidence of poleward flow and an incipient warm surface layer inshore occurred off Bodega Head on 25 June. Chl-a was generally low across the shelf, representative of newly upwelled waters, although a subsurface chlorophyll maximum was observed well offshore of Stewarts Point, beneath a warmer layer of oceanic water. Again on 14 July, active upwelling conditions were observed off Stewarts Point, with cold water shoaling to the surface nearshore and very low chl-a concentrations. At Bodega Head, farther from the upwelling center and a day later, some nearshore stratification and significant chl-a concentration was observed as well as weak surface currents (**Figure 3**).

Surface currents measured by HF radar showed that during the first pair of cruises on 28–29 May flow was poleward nearshore at Bodega Head and Stewarts Point; while offshore flow was observed at Point Arena, onshore flow of surface waters

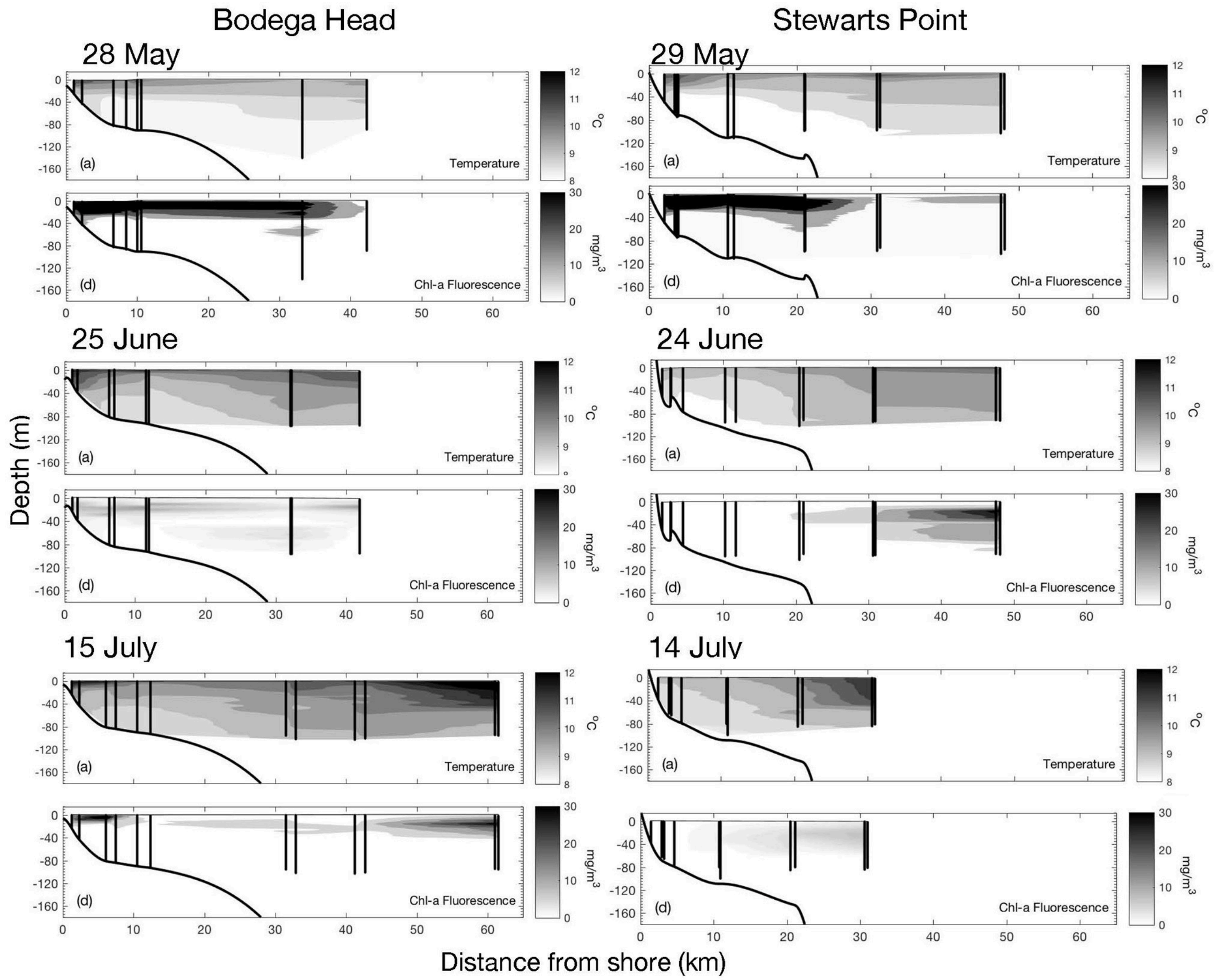

FIGURE 4 | Contours of temperature (°C) and chlorophyll-a from vertical profiles at six stations along transects off Bodega Head and Stewarts Point on 28–29 May, 24–25 June, and 14–15 July 2009. Profile locations at the beginning and end of plankton tows at each station are depicted by black vertical lines.

was observed south of Bodega Head (**Figure 3**). On June 24–25, nearshore flow was poleward from Bodega Head to Stewarts Point and equatorward from Point Arena to Stewarts Point where these currents converged, deflecting alongshore flow offshore. On July 14–15, nearshore flows were very weak in the vicinity of Bodega Head, but equatorward and offshore flow was well developed from Point Arena to south of Stewarts Point.

The progressive vector diagrams showed net poleward transport near-bottom and near-surface at both nearshore sites (**Figure 5**). Transport was shoreward near-surface and seaward near-bottom off Bodega Head, whereas it was seaward near-surface and near-zero near-bottom off Stewarts Point. At both sites, near-surface transport exhibited greatest excursions during upwelling and relaxation events, indicating that larvae remaining deep in the water column would travel the shortest distance.

Larvae of 42 species of benthic crustaceans generally did not occur farther offshore at the upwelling center at Stewarts Point than Bodega Head (**Figure 6**). Larvae largely occurred; l98.7989 < 11 km from shore at both sites, and early larval stages were abundant inshore where larvae are released. All stages of 22 species occurred on the inner shelf <11 km from shore off Bodega Head (99.8%) with the large majority of them occurring just 1 km from shore and most of the rest of them occurring 6 km from shore (**Figure 6**), revealing larval retention. Similarly off Stewarts Point, all stages of these species occurred on the inner shelf <10 km from shore (98.5%; **Figure 6**) with most of the rest of them occurring 3 km from shore. All stages of four more species occurred <11 km from shore off Bodega Head (96.1%) with the large majority of them occurring 1 km from shore and most of the rest of them occurring 6 km from shore while late stages occurred <32 km from shore (**Figure 6**). Similarly off Stewarts Point, all stages of these species occurred <10 km from shore (95.4%) with the large majority of them occurring just 1 km from shore and most of the rest of them occurring 3 km from shore while late

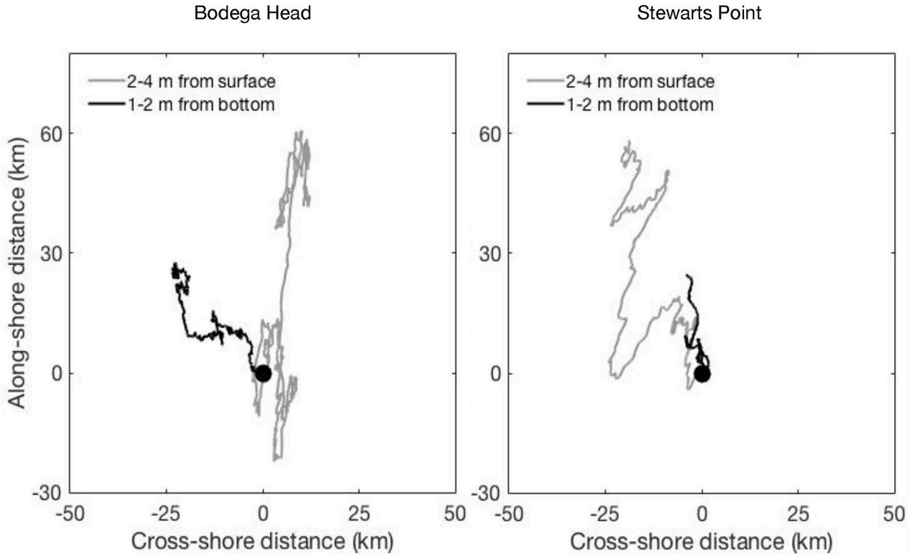

FIGURE 5 | Progressive vector diagrams of potential alongshore and cross-shore displacement due to currents measured near-surface (gray line) and near-bottom (black line) from mid 24 May through 26 July 2009 at Bodega Head and Stewarts Point. Current velocity was measured by a bottom-moored ADCP at 30-m depth at each site. Positive alongshore distances are poleward and positive cross-shore distances are shoreward.

stages occurred <30 km from shore (**Figure 6**). Early stages of 16 more species occurred <11 km from shore (81.8%) and late stages occurred far offshore in much lower abundance off Bodega Head (18.2 %, **Figure 6**). Similarly off Stewarts Point, early stages of these species occurred <10 km from shore (70.6%) and late stages occurred far offshore in low abundance (**Figure 6**). Thus, along both transects, larvae of most species were retained on the inner shelf while late stages other species ranged to the midshelf or offshore.

The 39 most abundant species differed primarily across stations (Bodega Head: ANOSIM $R = 0.439$, $p = 0.001$; Stewarts Point: ANOSIM $R = 0.373$, $p = 0.002$) but also among depths (Bodega Head: ANOSIM $R = 0.107$, $p = 0.096$; Stewarts Point: ANOSIM $R = 0.145$, $p = 0.055$), indicating that depth regulation contributed to interspecific differences in cross-shelf transport at both sites. Cluster analysis and nMDS showed pronounced spatial structure in larval assemblages along both transects grouping taxa into inner, mid and offshore categories for both transects with an outlier (neuston at Station 3) for the offshore group at Stewarts Point (**Figure 7**).

A nearshore cluster of all stages of 21 species largely occurred <6 km from shore (**Figures 7**, **8**), five species of porcelain crabs (*Petrolisthes cinctipes, Pet. eriomerus, Pet. manimaculus, Pachycheles rudis, Pac. pubescens*), a mud shrimp (*Neotrypaea californiensis*), five species of barnacles (*Balanus crenatus B. glandula, Semibalanus cariosus, Chthamalus dalli/fissus*), three hermit crabs (*Pagurus samuelis, P. hirsutiusculus, P. granosimanus*) and seven pea crabs (*Pinnixa faba, P. tubicola, Pinnotheres pugettensis, Scleroplax granulata, Fabia subquadrata*, two unidentified species). However, postlarvae of the three barnacles, three hermit crabs and seven pinnotherids occurred in very low concentrations to ∼18 km from shore during the cruise off Bodega Head on 28 May (**Figure 8**). Pinnotherid postlarvae occurred in low concentrations <30 km off Bodega Head and <20 km off Stewarts Point, because one of the species (*F. subquadrata*) disperses midshelf (Morgan et al., 2009c). Off Bodega Head, all stages of these species composed 12.9% of all larvae along the transect contributing 11.26% of the similarity to the cluster, and off Stewarts Point, all stages of these species composed 2.4% of all larvae collected along the transect and contributed 3.11% of the similarity to the cluster (**Figure 7**). Larvae of these species occurred below the shallow Ekman layer (**Figure 8**). Porcelain crabs undertook a ROVM (**Figure 8**) with similar ZCMs of larvae at the shallow stations inshore off Bodega Head (11.9 ± 3.0 m) and Stewarts Point (9.7 ± 4.6 m) and postlarvae ascending to the neuston (0.5 m) at both sites. In contrast, pinnotherid crabs undertook an OVM (**Figure 8**) with similar ZCMs of larvae inshore off Bodega Head (17.2 ± 3.2 m) and Stewarts Point (16.5 ± 3.5 m) and postlarvae descending much deeper in the water column (Bodega 49.0 m; Stewarts 37.4 ± 2.3 m). The rest of these species mostly occurred below the Ekman layer throughout development while perhaps undertaking an OVM with postlarvae occurring deeper than larvae on one or more cruises along both transects (**Figure 8**). *Neotrypaea californiensis* larvae occurred higher in the water column (14.5 ± 5.7 m) than postlarvae (24.0 ± 0.7 m) off Stewarts Point, though not off Bodega Head where both larvae (32.4 ± 15.0 m) and postlarvae (26.7 ± 8.9 m) occurred deeper than off Stewarts Point. Late-stage barnacle larvae were shallower (5.1 ± 2.3 m) than postlarvae (12.9 ± 1.0 m) off Bodega Head, though postlarvae were deeper on only one cruise off Stewarts Point. Similarly, hermit crab larvae were shallower (17.7 ± 0.6 m) than postlarvae off Bodega Head (46.8 ± 24.4 m), though postlarvae were deeper on only one cruise off Stewarts Point

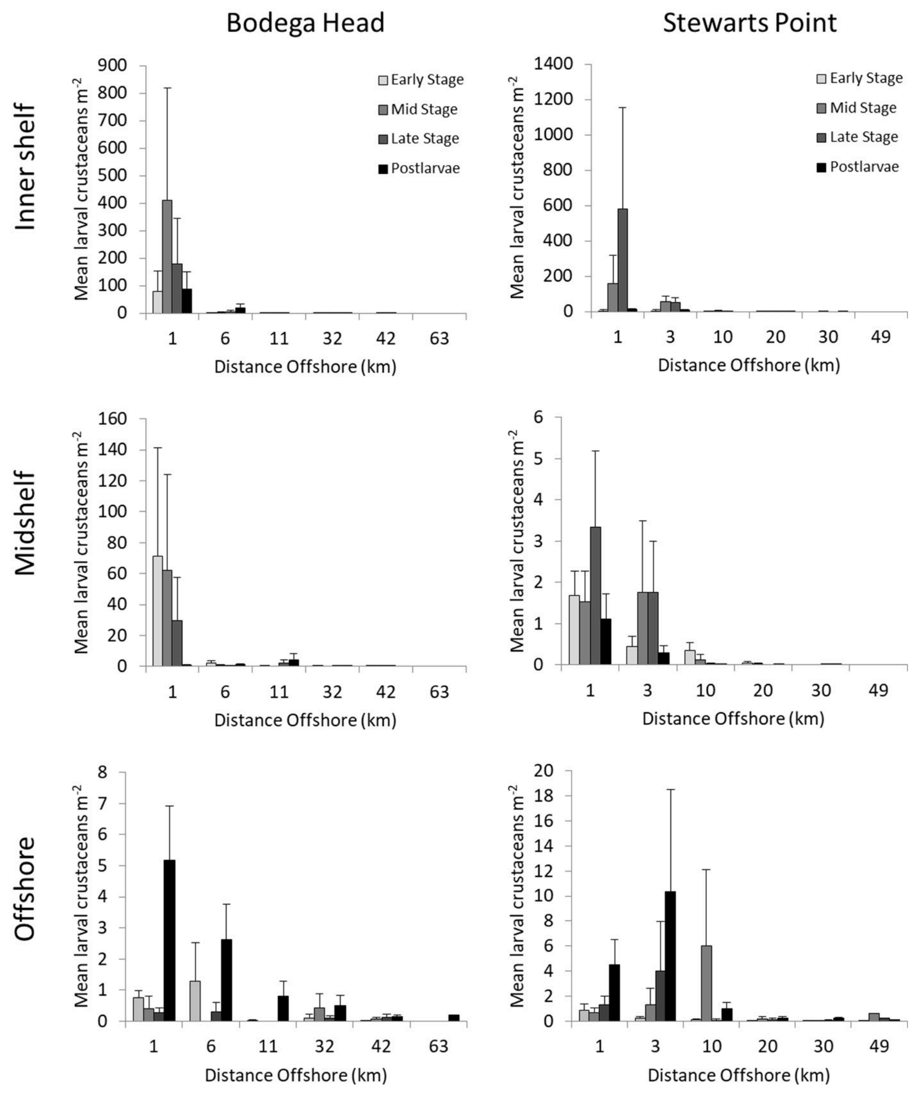

FIGURE 6 | Densities (mean/m^2 + 1 SE) of larval stages of 42 species of benthic crustaceans relative to distance from shore for all depths and cruises combined at Bodega Head and Stewarts Point on 28–29 May, 24–25 June, and 14–15 July. Twenty-two species largely remained on the inner shelf off Bodega Head (<11 km from shore) and Stewarts Point (<10 km from shore) throughout development. Four species primarily occurred on the inner shelf and ranged across the midshelf late in development off Bodega Head (<32 km from shore) and Stewarts Point (<30 km from shore). Sixteen species primarily occurred on the inner shelf and ranged offshore late in development off Bodega Head (>32 km) and Stewarts Point (>30 km). Note scale changes.

A midshelf cluster of all stages of four species largely occurred <6 km from shore with late stages occurring <32 km at both sites, including the xanthid crab *Lophopanopeus bellus*, two grapsid crabs (*Hemigrapsus oregonensis*, *H. nudus*) and *Romaleon* (*Cancer*) *antennarius* (**Figures** 7, **9**). Off Bodega Head, all stages of these species composed 85.1% of all larvae along the transect contributing 38.10% of the similarity to the cluster. Off Stewarts Point, all stages of these species composed 93.7% of all larvae collected along the transect and contributed 31.16% of the similarity to the cluster (**Figure** 7). The vertical distributions of *L. bellus* and the grapsid crabs were similar throughout development (**Figure 9**). ZCMs of *L. bellus* off Bodega Head were 14.0 ± 2.4 m for early larvae and 16.0 m for postlarvae (late stages were not collected), and ZCMs off Stewarts Point were 23.8 ± 5.5 m for early larvae, 27.9 m for late larvae and for 27.9 m postlarvae. Off Bodega Head, ZCMs of grapsid larvae were 13.1 ± 3.1 m for early stages, 14.6 ± 2.6 m for late stages and 12.6 m for postlarvae, and off Stewarts Point, ZCMs were 11.1 ± 1.0 m for early stages, 10.8 ± 1.8 m for late stages and postlarvae were not collected (**Figure 9**). Vertical distributions also were similar throughout development for *R. antennarius* off Bodega Head (early 23.3 ± 10.9 m, late 19.0 ± 3.0 m, postlarvae 17.8 ± 0.8 m), but there was evidence of a possible OVM off Stewarts Point with larvae occurring shallower (early 14.3 ± 5.5 m, late 15.2 ± 6.8 m) than postlarvae on two cruises (31.8 ± 6.8 m).

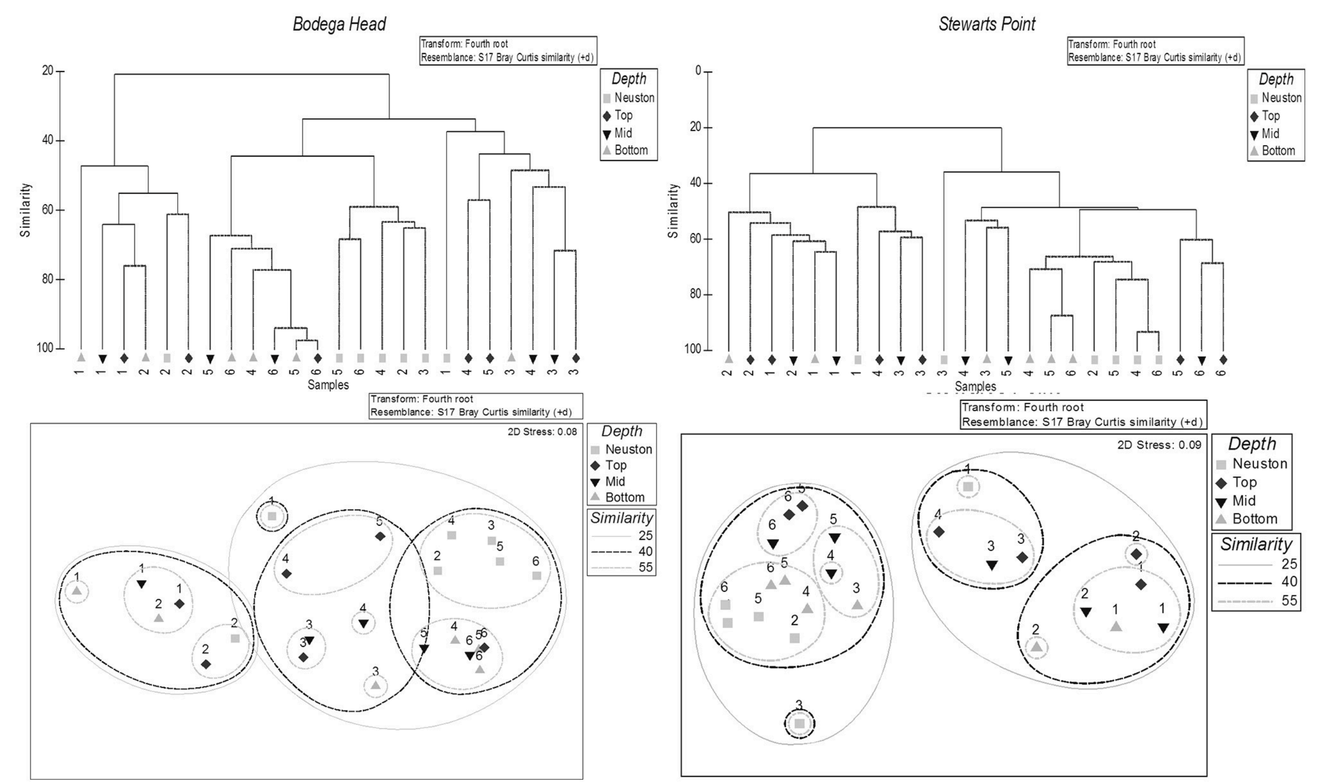

FIGURE 7 | Top panels. Hierarchical clustering dendrogram (using group-average linking) of 48 samples taken from four depths at six sampling stations across the continental shelf: 1, 6, 11, 32, and 63 km from shore off Bodega Head and 1, 3, 10, 20, 30, and 49 km from shore off Stewarts Point. Samples were categorized based on 25 and 40% similarities. Solid black lines indicate significant group structure at the 1% level. Sample distances offshore are reported beneath each group. **Bottom** panels: Nonmetric multidimensional scaling plots (2D stress: 0.08 for Bodega Head and 0.09 for Stewarts Point) from the 48 samples with superimposed significant clusters at similarity levels of 25% (solid lines) and 40% (dashed lines) off Bodega Head and Stewarts Point.

An offshore cluster composed of 14 species with early larval stages largely occurring <11 km from shore and late stages occurring >30 km from shore (**Figures 7**, **10**). Off Bodega Head, all stages of these species composed 1.9% of all larvae collected along the transect and contributed 49.36% of the similarity to the cluster, and off Stewarts Point, all stages of these species composed 3.4% of all larvae along the transect contributing 65.73% of the similarity to the cluster (**Figure 7**). Larvae of seven majiids (*Pugettia richii, P. producta, P. gracilis, Scyra acutifrons, Mimulus foliatus, Oregonia gracilis,* unidentified species) primarily completed development <11 km from shore, whereas larvae of three species of cancrid crabs [*Metacarcinus* (*Cancer*) *magister, Cancer productus, Glebocarcinus* (*Cancer*) *oregonensis*], two barnacles (*Balanus nubilus*, *Pollicipes polymerus*), *Emerita analoga* and an unidentified porcellanid occurred in low concentrations beyond 11 km (**Figures 7**, **10**). Larvae of these species commonly occurred in the Ekman layer midshelf and offshore (**Figure 10**). Cancrid postlarvae even were prevalent in the neuston at Station 3 off Stewarts Point (**Figure 10**), being reflected as an outlier for the offshore group off Stewarts Point in the dendrogram (**Figure 7**). The barnacles appeared to undertake an OVM (**Figure 10**); ZCMs were shallower for late-stage barnacle larvae (Bodega 15.3 ± 0.1 m; Stewarts 15.6 ± 2.8 m) than postlarvae (Bodega 30.5 ± 3.6 m; Stewarts 27.2 ± 4.5 m). Majiids may have undertaken an OVM (**Figure 10**). Off Bodega Head, ZCMs of majiid larvae were shallower (early 11.7 ± 1.6 m, late 11.1 ± 1.1) than postlarvae (21.9 ± 15.8 m), and off Stewarts Point, early-stage larvae also were shallower (15.8 ± 5.3 m) than late-stage larvae (20.6 ± 13.4) and postlarvae (22.1 ± 2.3 m). Cancrids may have undertaken a ROVM (**Figure 10**). Cancrid larvae off Bodega Head were deeper (early 12.0 ± 0.4 m) than postlarvae (0.5 m), and this also was the case off Stewarts Point (early 22.2 ± 10.9 m, late 13.8 ± 1.0 m), except during one cruise when postlarvae occurred in low concentrations ~45 m deep resulting in a ZCM of 20.2 ± 13.1 m. *Emerita analoga* larvae commonly occurred in the surface layer across the shelf (**Figure 10**) with ZCMs off Bodega Head of 6.7 ± 2.2 m for early larvae and 12.5 m for late larvae and ZCMs off Stewarts Point of 15.0 m for late larvae. Unidentified porcellanid larvae also occurred in the surface layer across the shelf off Stewarts Point with ZCMs of 0.5 m for early larvae and 10.0 m for late larvae, but early stages were deep in the water column during the one cruise that they were collected off Bodega Head with a ZCM of 59.4 m (**Figure 10**). We did not detect ontogenetic changes in vertical distributions of *E. analoga*

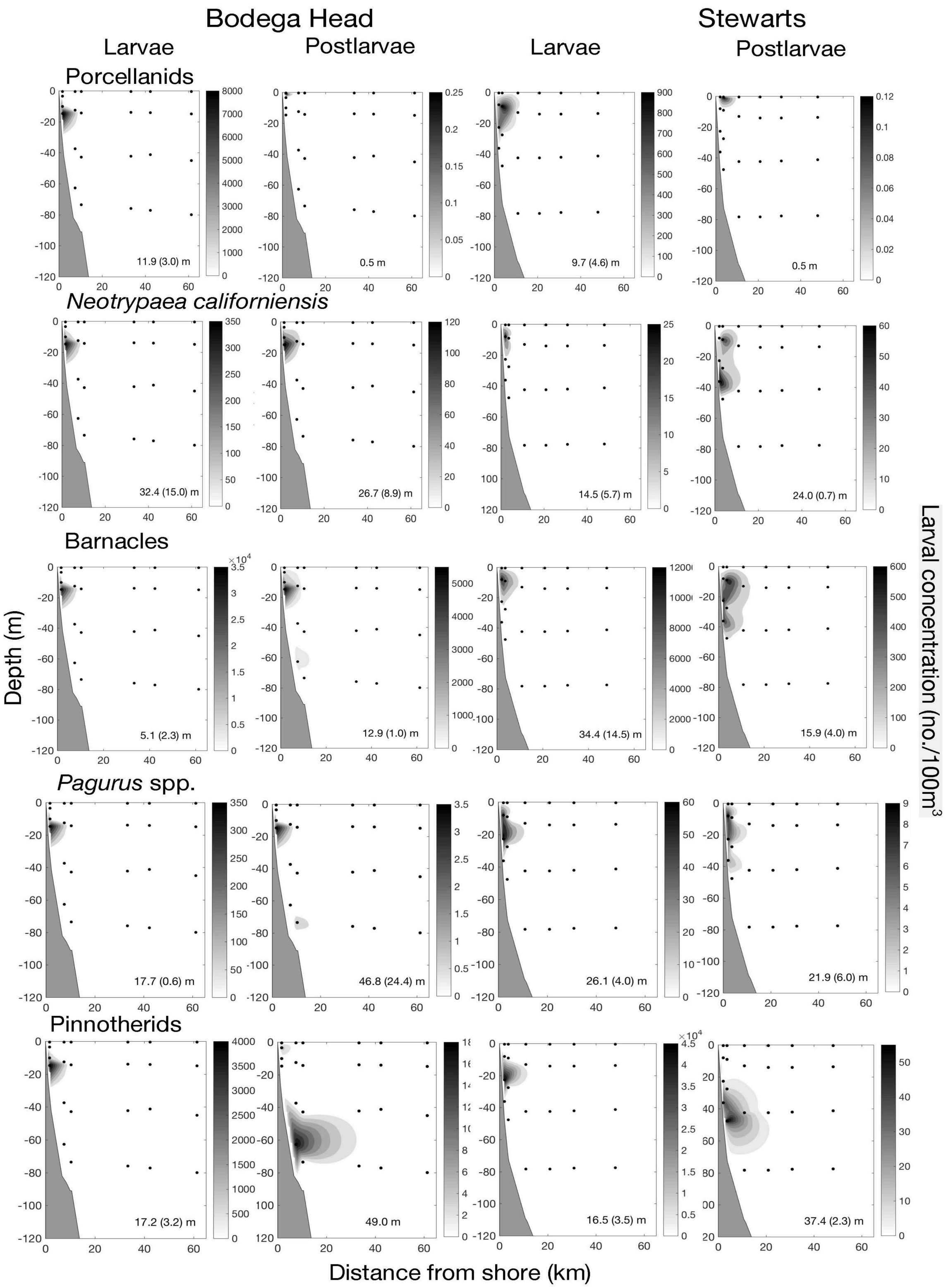

FIGURE 8 | Inner-shelf larval development of 21 species in relation to distance from shore and depth off Bodega Head and Stewarts Point for larvae that largely occurred <6 km. First row of panels for five species of porcelain crabs (*Petrolisthes cinctipes, Pet. eriomerus, Pet. manimaculus, Pachycheles rudis, Pac. pubescens*); second row of panels for a mud shrimp (*Neotrypaea californiensis*); third row of panels for five species of barnacles (*Balanus crenatus B. glandula, Semibalanus cariosus, Chthamalus dalli/fissus*); fourth row of panels for three hermit crabs (*Pagurus samuelis, P. hirsutiusculus, P. granosimanus*); and fifth row of panels for seven

(Continued)

FIGURE 8 | pea crabs *(Pinnixa faba, P. tubicola, Pinnotheres pugettensis, Scleroplax granulata, Fabia subquadrata*, two unidentified species). The depth center of mass (ZCM; mean with SE in parentheses) is given at the bottom of each panel. ZCM with no variation shown in parentheses indicates species were collected during a single cruise, and separate groups of larvae within panels were collected during different cruises. Missing panel indicates that small larvae passed through nets.

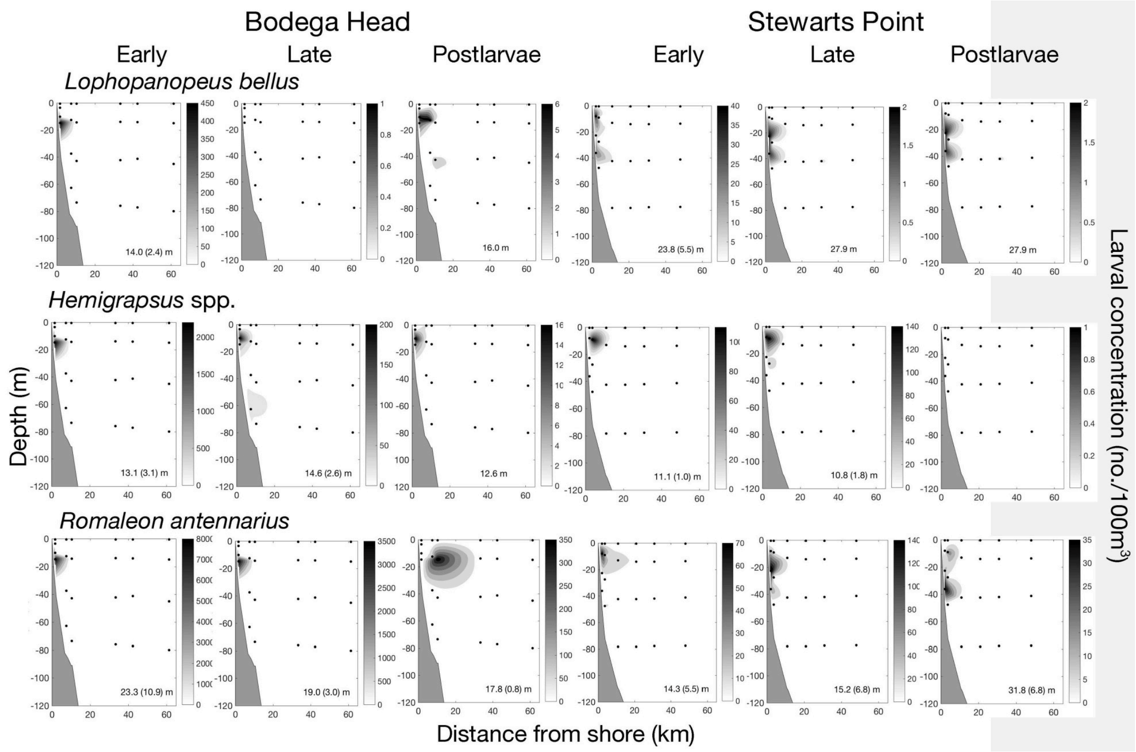

FIGURE 9 | Midshelf larval development of four species in relation to distance from shore and depth off Bodega Head and Stewarts Point where larvae largely occurred <11 km from shore with late stages primarily occurring <32 km. First row of panels for the xanthid crab *Lophopanopeus bellus;* second row of panels for two grapsid crabs (*Hemigrapsus oregonensis, H. nudus*); and third row panels for a rock crab *Romaleon* (*Cancer*) *antennarius*. The depth center of mass (ZCM; mean with SE in parentheses) is given at the bottom of each panel. ZCM with no variation shown in parentheses indicates species were collected during a single cruise, and separate groups of larvae within panels were collected during different cruises. Missing panel indicates that small larvae passed through nets.

or the unidentified porcellanid because we did not collect postlarvae.

DISCUSSION

We have shown that larvae of nearshore benthic crustaceans are retained nearshore or reliably migrate different distances from shore during the season of peak upwelling and in the core of an upwelling center within the region of the most persistent, strongest upwelling along the Pacific Coast of North America. In this work and previous studies, we have repeatedly sampled larval assemblages during many cruises over multiple locations and years (Morgan et al., 2009b,c; Morgan and Fisher, 2010; Hameed et al., 2018). In this work, we focused on the time and place of maximum upwelling, showing that larvae were not transported farther offshore at this region of strong, persistent upwelling, contrary to widespread expectations. During the present study, we sampled larvae of 42 nearshore benthic crustaceans and 99; l98.7989% of all larvae were collected over the inner shelf, <11 km from shore along both transects. Larvae were most concentrated within a few kilometers of the shoreline, in the coastal boundary layer where offshore Ekman transport and alongshore currents are weak (Lentz and Chapman, 1989; Largier et al., 1993; Kaplan et al., 2005; Kirincich et al., 2005; Roughan et al., 2006; Morgan et al., 2009c; Morgan and Fisher, 2010; Nickols et al., 2012, 2013; Hameed et al., 2018). Not only was this characteristic coastal-boundary-layer circulation (Pettigrew and Murray, 1986; Shanks, 1995a; Largier, 2002, 2003) persistent, but it is expected to contribute to nearshore larval retention of diverse benthic crustaceans in other upwelling regions worldwide (Morgan, 2014).

All larval stages of 21 species occurred in high concentrations primarily in the coastal boundary layer <6 km offshore, including the five species of porcelain crabs, mud shrimp, five species of barnacles, three hermit crabs and seven pea crabs. The three species of barnacles, three species of hermit crabs and six of the seven species of pinnotherids in this nearshore group also completed development in high concentrations <6 km from

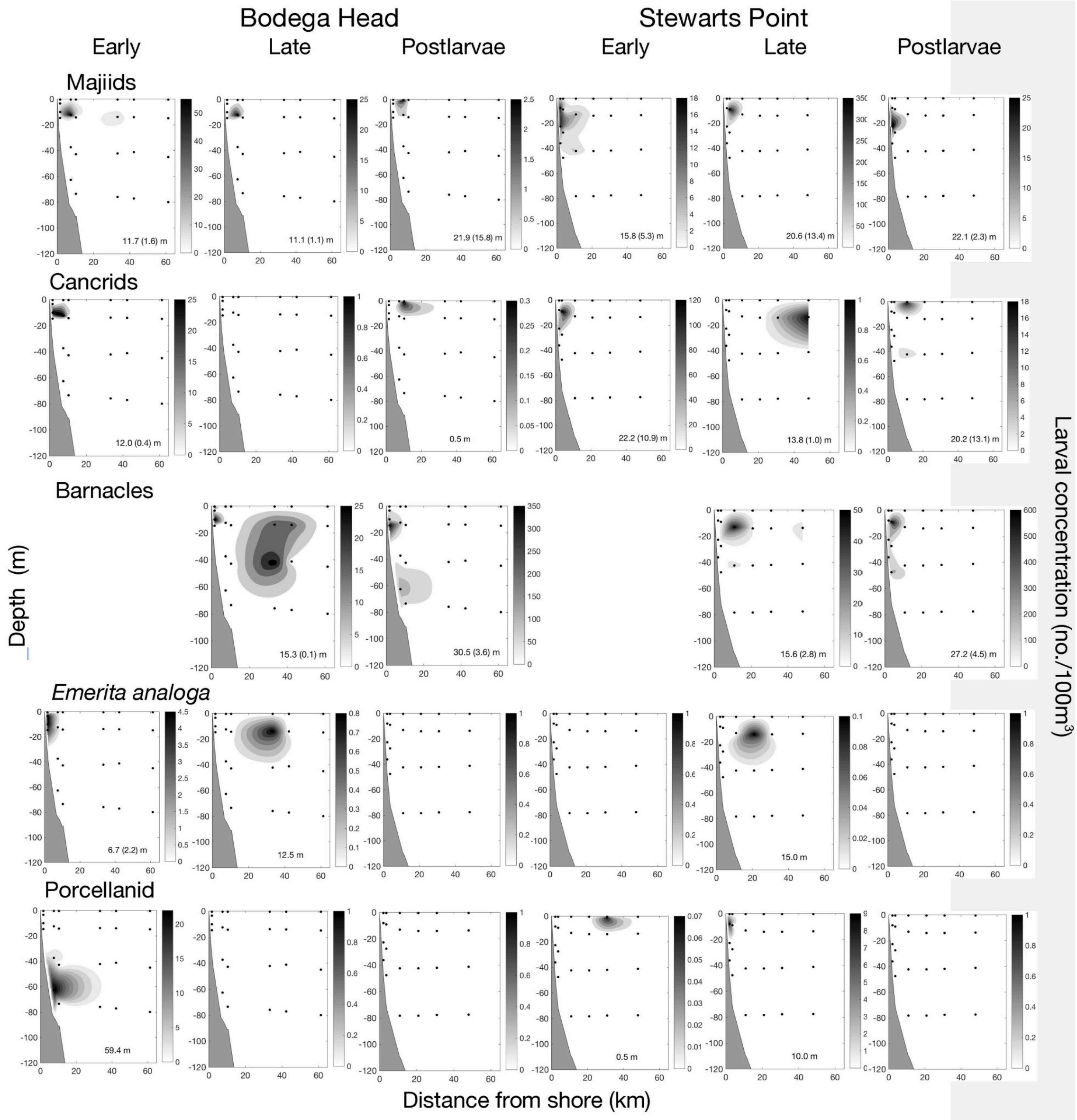

FIGURE 10 | Offshore larval development of 14 species in relation to distance from shore and depth off Bodega Head and Stewarts Point where larvae largely occurred <11 km from shore with late stages occurring >32 km from shore. First row of panels for seven majid crabs (*Pugettia richii, Pugettia producta, Pugettia gracilis, Scyra acutifrons, Mimulus foliatus, Oregonia gracilis,* unidentified species); second row of panels for three cancrid crabs (*C. magister, C. productus, C. oregonensis*); third row of panels for two barnacles (*Balanus nubilus, Pollipes polymerus*); fourth row of panels for the mole crab (*Emerita analoga*); and fifth row of panels for an unidentified porellanid. The depth center of mass (ZCM; mean with SE in parentheses) is given at the bottom of each panel. ZCM with no variation shown in parentheses indicates species were collected during a single cruise, and separate groups of larvae within panels were collected during different cruises. Missing panel indicates that small larvae passed through nets.

shore off Bodega Head in our previous studies (Morgan et al., 2009b,c; Morgan and Fisher, 2010; Nickols et al., 2013; Hameed et al., 2018). In our present study, these barnacles and hermit crabs completed development close to shore in five of the six cruises, but in the 28 May cruise off Bodega Head their postlarvae were found in very low concentrations up to ∼18 km from shore. This survey was conducted during a relaxation event when a poleward flow from the Gulf of Farallones can transport plankton offshore north of Point Reyes, unlike during prevailing upwelling conditions (Kaplan and Largier, 2006; Morgan et al., 2012). In addition, one of the seven pinnotherids (*F. subquadrata*) developed farther from shore than the other six species in our previous study off Bodega Head, but we did not distinguish it from the other pinnotherids during the present study.

Of the species that did not complete their larval life nearshore, many occurred in high concentrations <11 km early in development and in lower concentrations farther from shore late in development. The four species that occurred midshelf (*L. bellus*, *Hemigrapsus* spp., *R. antennarius*) or the 14 species that occurred offshore (seven majiids, three cancrids, two barnacles, mole crab, unidentified porcellanid) late in development had similar distributions in our previous studies (Morgan et al., 2009b,c; Morgan and Fisher, 2010; Nickols et al., 2013; Hameed et al., 2018). Postlarvae of all of these species spanned the continental shelf while recruiting onshore. Crustacean larvae had similar cross-shelf distributions off Oregon (Lough, 1974; Fisher et al., 2014), indicating that these interspecific differences are maintained in time and space.

Distinctive vertical distributions of larval stages were related to horizontal distributions likely contributing to maintaining the three cross-shelf patterns. Larvae in the nearshore group occurred deep in a shallow water column early in development and most species either descended (*N. californiensis*, *B. crenatus*, *B. glandula*, *Pagurus* spp., pinnotherids) or ascended (porcellanids) late in development apparently undertaking an OVM or ROVM, respectively. Similar ontogenetic changes in vertical distributions were evident in our previous study off Bodega Head, and in addition, *Chthamalus* spp. underwent a ROVM (Morgan et al., 2009c). The subsurface vertical distributions of all these larvae and postlarvae undertaking an OVM (in this and prior studies) placed them in onshore and weak alongshore flow (Largier et al., 1993; Dever et al., 2006; Roughan et al., 2006; Nickols et al., 2012), likely facilitating retention nearshore (Peterson, 1998; Batchelder et al., 2002; Papastephanou et al., 2006; Morgan et al., 2009c; Morgan and Fisher, 2010; Nickols et al., 2013; Hameed et al., 2018). Barnacle and pinnotherid larvae typically stay deep, whereas *N. californiensis* and *Pagurus* spp. larvae rise near the surface at night (Morgan and Fisher, 2010) after winds subside and are often onshore reducing transport (Peterson et al., 1979; Hobbs et al., 1991; Peterson, 1998; Batchelder et al., 2002; Poulin et al., 2002; Marta-Almeida et al., 2006; dos Santos et al., 2008; Bonicelli et al., 2016). By undertaking a ROVM, postlarvae of the porcellanids and *Chthamalus* spp. could be transported shoreward by winds and internal tides in the neuston (Pineda, 1994, 1999; Shanks, 1995a), which occur in our region during relaxation periods in a stratified water column (Rosenfeld, 1990).

Early stages of the rest of the species were transported farther from shore by spending more time in surface currents (Morgan et al., 2009c; Morgan and Fisher, 2010), as do copepods (Peterson et al., 1979; Peterson, 1998; Batchelder et al., 2002; Papastephanou et al., 2006). Ten species (*R. antennarius*, two barnacles, seven majiids), generally descended into deeper onshore flow late in development during our present or previous study (Morgan et al., 2009c). Onshore transport of late stages limits cross-shelf displacement and returns postlarvae to shore (Peterson et al., 1979; Grantham, 1997; Peterson, 1998; Papastephanou et al., 2006; Morgan et al., 2009c). The three species of cancrids transported offshore returned to shore as postlarvae by ascending to the neuston. Ontogenetic vertical migrations either were not apparent (*L. bellus*) or indeterminate without all larval stages being collected (*E. analoga*, unidentified porcellanid) in this or our previous study (Morgan et al., 2009c). Even without ontogenetic changes in vertical distributions, crabs in this region generally rise near the surface at night (Morgan and Fisher, 2010) facilitating onshore transport by internal tides and winds (Jamieson and Phillips, 1988; Shenker, 1988; Hobbs et al., 1991; Shanks, 1995b; Rasmuson and Shanks, 2013).

As we discussed previously (Morgan et al., 2009c; Fisher et al., 2014; Morgan, 2014), passive advection and eddy diffusion alone cannot explain the differences in cross-shelf distributions among so many species, because (1) these larvae are released inshore and encounter the same physical processes, (2) distances larvae migrate from shore are not related to larval durations, (3) larval densities were adjusted to account for increasing depth across the shelf to ensure that high larval concentrations after hatching were not simply reduced by dilution due to vertical mixing as the water column deepened offshore and (4) late stages were as abundant or increased midshelf and offshore instead of decreasing. Thus, behavior is common across larval taxa and many species exhibit behaviors that reduce offshore transport in upwelling regions elsewhere on the Pacific Coast, including in the weaker upwelling off Oregon (Peterson et al., 1979; Shanks and Shearman, 2009; Fisher et al., 2014) and central through southern California (Grantham, 1997; Tapia and Pineda, 2007), as well as worldwide, including Chile (Poulin et al., 2002; Bonicelli et al., 2016) and the Iberian Peninsula (Marta-Almeida et al., 2006; dos Santos et al., 2008; Bartilotti et al., 2014).

If larvae remain close to shore, why are populations recruitment limited in persistent, strong upwelling regions? Presumably, there is a constraint between the larval availability in the plankton over the inner shelf and the settlement of benthic larvae in shoreline habitats. Recent work has shown that the ability of postlarvae to enter the surf zone largely depends on temporal and spatial variation in surfzone hydrodynamics, which is determined by breaking waves interacting with alongshore changes in coastal morphology, yielding a spectrum of surf zones from dissipative to reflective (Wright and Short, 1984). Broad surf zones along mildly sloping shorelines usually have far more larvae and other plankton and much greater settlement onshore (Shanks et al., 2010, 2017, 2018, in press; Morgan et al., 2016, 2017, 2018). These dissipative surfzones have bathymetric rip currents, which concentrate plankton by recirculation in a series of rip currents alongshore, unlike narrow reflective surf zones at steep shores (Shanks et al., 2010, 2017, 2018, in press; Morgan et al., 2016, 2017, 2018). Individual based biophysical models revealed that Stokes drift and benthic boundary layer streaming coupled with downward swimming in response to turbulence from waves facilitated onshore larval delivery beaches (Fujimura et al., 2013, 2014, 2017, 2018). The striking differences in surfzone oceanography at dissipative and reflective shores predictably affect larval recruitment and productivity of inshore communities (Morgan et al., 2016, 2017, 2018; Shanks et al., 2017, in press) and appear to explain recruitment limitation at many sites in California (Morgan et al., 2016, 2017; Shanks et al., 2017; Shanks and Morgan, 2018). Together with the above results on larval distributions in upwelling areas, this suggests a shift in paradigms from the past idea that upwelling necessarily limits recruitment to new ideas that recruitment limitation and population connectivity may be better explained by alongshore differences in surfzone circulation (Shanks et al., 2017; Shanks and Morgan, 2018; Morgan, in press).

Larval retention evidently occurs all along coasts in upwelling regions, rather than primarily occurring in bays and eddies in the lee of headlands. This implies that alongshore transport and the scale of connectivity in benthic metapopulations in upwelling areas is less than previously suggested. Larval transport would be reduced even further if postlarvae effectively navigate onshore in upwelling regimes. Elsewhere, postlarvae can navigate onshore to suitable settlement sites using hierarchies of cues that are effective over different spatial scales, including celestial bodies, polarized light, magnetic and electric fields, waves and tides, and acoustic, chemical and visual cues (Kingsford et al., 2002; Montgomery et al., 2006; Arvedlund and Kavanagh, 2009; Morgan, in press). Adding onshore navigation into individual based biophysical models in upwelling regions (Pfeiffer-Herbert et al., 2007; Carr et al., 2008; Petersen et al., 2010; Domingues et al., 2012; Drake et al., 2013; Nolasco et al., 2013) should reduce the scale of population connectivity even further, but onshore navigation remains to be documented for species in upwelling regimes (Morgan, in press). The ultimate goal is to determine realized population connectivity, reconciling evidence from studies of circulation, plankton, genetics and microchemistry. Next steps should also include incorporating documented reproductive outputs of a metapopulation (Hameed et al., 2016), larval behaviors documented here and previously (Morgan et al., 2009b; Morgan and Fisher, 2010) and larval mortality rates (White et al., 2014) into the numerical circulation model (Regional Ocean Modeling System; Drake et al., 2013). This would provide one of the first reliable estimates of realized population connectivity (Burgess et al., 2014). Clearly, a fresh look at the underlying processes responsible for spatial and temporal patterns of recruitment and population connectivity for diverse taxa and locations across upwelling coasts is needed to better understand the regulation of marine populations and communities (Shanks et al., 2017; Morgan et al., 2018; Shanks and Morgan, 2018).

In conclusion, larval retention is likely commonplace all along upwelling coasts with larvae recruiting closer to home and more abundantly than has been widely appreciated. Here, we demonstrated that this is even true at locations and times when upwelling is strongest, such as in the Point Arena upwelling center. This deeply affects the ecology, evolution and management of species in upwelling regimes. More larval retention should increase coupling between stock and recruitment, local adaptation and local benefits of marine protected areas as well as vulnerability of marine protected areas to overfishing and other disturbances (Strathmann et al., 2002; Sanford and Kelly, 2011; Burgess et al., 2014, 2016).

AUTHOR CONTRIBUTIONS

SGM: Conceived of the research; SGM and JL: Were awarded funding to conduct the study; SHM, SGM, and MR: Conducted the study; SHM and MR: Processed, analyzed and graphed the data with SGM; SGM: Wrote the ms with input by all.

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Wind Conditions on the Great Barrier Reef Influenced the Recruitment of Snapper (*Lutjanus carponotatus*)

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Most coral reef fishes have a pelagic larval stage before recruiting to reefs. The survival of larvae and their subsequent recruitment can drive the dynamics of reef populations. Here we show that the recruitment of the snapper *Lutjanus carponotatus* to One Tree Island in the Capricorn Bunker Group, in the southern Great Barrier Reef, was highly variable over 23 years. We predicted that the currents in the Capricorn Bunker Group, including their wind driven components and the Capricorn Eddy (a nearby transient oceanic eddy), would affect patterns of recruitment. A biophysical model was used to investigate this prediction. *L. carponotatus* were collected from One Tree Island and the dates when they were in the plankton as larvae were determined from their otoliths. The winds present during the pelagic phases of the fish were examined; they were found to have survived either longshore (SSE) winds that induced little cross shelf movement in the larval plume or cross shelf (ENE) winds that induced little longshore movement. The unidirectional transportation of the larval plume in these conditions was favorable for recruitment as it kept the plume concentrated in the Capricorn Bunker Group. These winds were more prevalent in the periods of peak *L. carponotatus* production that preceded high recruitment. Dispersal under average winds (6.2 m s^{-1} from the prevailing ESE) and strong winds (velocity 1.5 times average), with and without the Capricorn Eddy, was also modeled. Each of these combinations were less favorable for recruitment than the longshore and cross shelf winds larval *L. carponotatus* survived before reaching OTI. The larval plume was comparatively less concentrated in the Capricorn Bunker Group under average winds. Strong winds transported the larval plume far longshore, to the NW, away from the Capricorn Bunker Group, while the Capricorn Eddy transported larvae seaward into oceanic waters. Larval swimming could counteract these dispersive forces; however, significant dispersion had occurred before larvae developed strong swimming and orientation abilities. This study provides a physical proxy for the recruitment of snapper. Further, we have demonstrated that great insights into recruitment variability can be gained through determining the specific conditions experienced by survivors.

Keywords: biophysical model, recruitment, wind, SLIM, stripey snapper (*Lutjanus carponotatus*)

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INTRODUCTION

Most coral reef fishes have bipartite lifecycles, where adults produce large numbers of larvae that spend some time developing in the plankton before metamorphosing, settling and recruiting to reefs. Recruitment is the raw material for post-settlement processes. It can be a fundamental driver of the population dynamics of coral reef fishes, especially for relatively short-lived species (e.g., Victor, 1983; Kingsford, 2009). Only a small fraction of the larvae produced by coral reef fishes will survive the pelagic phase (Houde, 2008). As large numbers of larvae are produced, small changes in the pre-settlement mortality rate can greatly affect the strength of recruitment events (Cowen et al., 2000; Houde, 2008). The pre-settlement mortality rate of fish larvae can depend on multiple factors including the availability of food (e.g., Cushing, 1975, 1990), the abundance of predators (e.g., Moller, 1984; McGurk, 1986) and favorable or unfavorable oceanography (e.g., Sponaugle and Pinkard, 2004; Sponaugle et al., 2005), and this complexity can make it difficult to identify causes of variability in recruitment (Leggett and Deblois, 1994; Houde, 2008).

Flow fields can influence the magnitude of recruitment over multiple spatial scales. For example, at small spatial scales, tidal eddies regularly form as tidal currents flow past reefs and these eddies can retain larvae (Burgess et al., 2007). Furthermore, water circulation can be reduced in dense reef matrices (the "sticky water effect") and larvae can be retained in this slow moving water (Andutta et al., 2012). Alternatively, currents can expatriate fish larvae away from suitable habitat, leading to poor recruitment (Sinclair, 1988; Lenanton et al., 1991; Fletcher, 1995).

In addition to physical oceanographic features, the biological characteristics of fish larvae can greatly affect their dispersion (Kingsford et al., 2002; Paris et al., 2013; Wolanski and Kingsford, 2014; Bottesch et al., 2016). The larvae of many fish species can maintain swim speeds that exceed local mean current speeds for extended periods of time, they can, therefore, influence their dispersal trajectories (Fisher, 2005; Leis, 2006). They can also orient to reefs using a variety of senses including a sun compass (e.g., Leis and Carson-Ewart, 2003; Mouritsen et al., 2013) and a magnetic compass (e.g., Bottesch et al., 2016) for long distance orientation, and hearing (e.g., Mann et al., 2007; Wright et al., 2010) and chemotaxis (e.g., Gerlach et al., 2007; Dixson et al., 2008; Paris et al., 2013) when they are closer to reefs. The exceptional swimming and orientation abilities of reef fish larvae, in combination with hydrodynamic retention mechanisms near reefs, may prevent the expatriation of some larvae away from natal reefs (Almany et al., 2007; Andutta et al., 2012). Indeed, high rates of self-seeding have been reported in local populations of coral reef fishes (Jones et al., 1999; Almany et al., 2007). However, many larvae will not return to their natal reefs and dispersal kernels (the potential for successful dispersal connections) can extend tens to hundreds of kilometers from the spawning of adults (Jones, 2015; Williamson et al., 2016).

Given the complex oceanographic regimes of coral reef ecosystems and the considerable swimming and orientation abilities of fish larvae, biophysical modeling is an ideal technique for investigating variability in recruitment (Simpson et al., 2013; Wolanski, 2017). Biophysical models combine oceanographic and behavioral models. They have been utilized to model connectivity and recruitment variability in coral reef systems to great effect (e.g., Paris and Cowen, 2004). They have also been used extensively to investigate the recruitment of commercially important species to fisheries (e.g., Caputi et al., 1996; Hare et al., 1999). Biophysical models are useful tools for making predictions on self-seeding and connectivity between populations at biologically relevant spatial and temporal scales, which can aid in the management of coral reef fish populations (Cowen et al., 2006; Melbourne-Thomas et al., 2011).

The inherent stochasticity and complexity of coral reef systems is not always well captured in biophysical models (Siegel et al., 2003, 2008). The models are typically forced with general physical conditions. While this approach is useful for reaching broadly applicable conclusions, great insights can be gained from using tailored forcings to answer specific questions (e.g., Mitarai et al., 2008). High variability in recruitment, both within and among seasons, appears to be typical of many coral reef systems (e.g., Doherty, 1987; Tolimieri et al., 1998). A comprehensive understanding of recruitment variability can be attained through investigating the conditions present when successful recruits were known to be in the plankton (Sponaugle and Pinkard, 2004; Valles et al., 2009). Accordingly, the causal factors of recruitment variability could be investigated by forcing a biophysical model with the conditions present during the pelagic larval phases of successful recruits.

Stripey snapper, *Lutjanus carponotatus*, is a predatory coral reef fish that is also targeted by fisheries. The recruitment of *L. carponotatus* to One Tree Island (OTI) in the Capricorn Bunker Group (CBG) in the southern Great Barrier Reef (GBR) has been monitored since 1995, and has been found to vary greatly interannually (Kingsford, 2009). The complex oceanography of the region could potentially affect the strength of recruitment events. The Capricorn Eddy (CE), a large, transient mesoscale oceanic eddy, forms offshore of the CBG (Weeks et al., 2010; Mao and Luick, 2014). It is presumably ecologically important as it upwells cool nutrient rich water to the surface (Weeks et al., 2010) and mesoscale eddies can greatly influence the dispersal trajectories of fish larvae (Sponaugle et al., 2005). Additionally, the CBG lies on a shallow section of the Australian continental shelf, and the surface currents in this region are largely wind driven (Andutta et al., 2013; Mao and Luick, 2014). A biophysical model has previously been used to simulate the dispersion of larvae seeded from OTI, and the subsequent recruitment of the larvae to OTI and to nearby downstream reefs (Wolanski and Kingsford, 2014). The dispersal trajectories of larvae were found to be greatly influenced by swimming behavior.

The broad objective of this study was to determine the conditions experienced by *L. carponotatus* larvae before they successfully recruited to OTI. Identifying the conditions that facilitated recruitment could improve our current understanding of the inter-annual variability in recruitment that is common among coral reef fishes. The specific aims were to: (1) examine the otoliths of successful *L. carponotatus* recruits caught from OTI to determine when they were in the plankton as larvae; (2) identify the wind conditions that fish experienced on these dates; (3) establish if the prevalence of these conditions could be used as a proxy to predict recruitment; (4) use biophysical modeling to determine the influence of wind, the CE and the swimming behavior of larvae on patterns of recruitment. Further, we hypothesized that the wind conditions survived by successful recruits during their larval phase (as identified in specific aim 2) would generate currents that reduced larval morality via expatriation, facilitating recruitment. We evaluated this hypothesis in specific aim 4 by modeling the identified winds.

MATERIALS AND METHODS

The Long-Term Abundance of *Lutjanus carpontatus* at One Tree Island

One Tree Island (OTI) is a small coral cay, located on the eastern side of a ∼5.5 km by 3.5 km coral reef (23°29′48.38″S, 152°4′8.32″E; **Figure 1**). OTI is in the Capricorn Bunker Group (CBG), within the southern Great Barrier Reef (GBR). The CBG lies near the edge of the Australian continental shelf, in waters approximately 50 m deep.

Lutjanus carponotatus have been counted in visual surveys performed in reef slope, lagoon edge and lagoon center habitats at OTI in January or February of each year since 1995. Counts were made at six or seven sites per habitat in five 5 × 25 m transects per site (for complete methods see Kingsford, 2009). Fish were not counted in the lagoon center habitat in 1998 and 1999, and they were not counted in the reef slope habitat in 2014, but *L. carponotatus* are rare in this habitat. The Standard Lengths (SL's) of the fish were estimated to the nearest 50 mm and these measurements were used to divide the fish into size categories. Length estimates were cross-checked by measuring the lengths of speared fish ($n = 114$) and, for consistency, Kingsford conducted all of the fish counts. Kingsford (1998) found that experienced divers could place large fish into the correct 50 mm size category 80% of the time. Further, in studies on smaller species (less than 300 mm), experienced divers may be able to consistently estimate lengths to within 10 mm of the true value (Kingsford, 1998). It is therefore acceptable to collect size-frequency data in 50 mm size categories (Kingsford, 1998). Fish with SL's greater than 200 mm were classified as adults. Most *L. carponotatus* of this size (200 mm SL ∼ 237 mm FL) are mature (Kritzer, 2004) and have three or more annulus bands on their otoliths (Kingsford, 2009), suggesting they have lived through at least three winters (Newman et al., 1996). Fish with SL's less than 150 mm were classified as recruits as most *L. carponotatus* of this size (150 mm SL ∼ 177 mm FL) are immature (Kritzer, 2004) and have no or only one annulus band on their otoliths (Kingsford, 2009), suggesting they are yet to live through a winter or have only lived through one (Newman et al., 1996).

Although there are no data available on the sources of *L. carponotatus* recruits to OTI, it was possible that the abundance of recruits would vary with the abundance of adult *L. carponotatus* at OTI as dispersal kernels tend to decrease rapidly with distance from the natal reef (e.g., Buston et al., 2012; Williamson et al., 2016). Accordingly, the relationship between recruit abundance (1996–2017) and adult abundance (1995–2016) was tested using a Spearman's Correlation. A Spearman's Correlation was performed because the data did not meet the Pearson's Correlation assumption of a bivariate normal distribution. A one-year time lag was applied as the recruits observed in any given year would have been produced by the adult population present in the previous year. Adult and recruit abundance data from 1998 and 1999 were not included as the lagoon center habitat was not sampled in these years. Recruit abundance data from the reef slope habitat were not included as no recruits were observed in this habitat. The adult abundance data from 2014 were not included as the reef slope habitat was not sampled in this year.

Otolith Analysis

Thirty-Five *L. carponotatus* were caught at OTI, either with spear-guns and hand spears (February 2004/2005, $n = 12$ recruits) or in light traps over the reef slope (January 2015, $n = 23$ potential settlers). These fish were caught opportunistically so samples were only available in some years. The fish had survived the hydrodynamic conditions present during their planktonic phases. It was, therefore, hypothesized that the currents, including their wind driven components, had facilitated their successful recruitment to OTI from their unknown sources. The dates when the fish were in the plankton were determined from the pre-settlement phases recorded on their otoliths. Sagittal otoliths were removed from the 35 *L. carponotatus* and sectioned following Kingsford (2009). Photographs of the otoliths were taken at 400 times magnification using a Leica microscope camera and the daily rings were counted from the photographs using Leica IM50 software. Counts were made from the hatch marks at the cores of the otoliths to the edges. The otoliths were examined in random order twice, with each session separated by a few weeks. If the counts differed by more than 10%, the otoliths were re-examined a third time. The third count was used if it was within 10% of either of the previous counts. The average of the closest counts was taken as the age of the recruit. Only one otolith was rejected via this method.

It was assumed that the fish hatched approximately 1 day after they were spawned, which is well within the range of hatching times recorded for other lutjanid species (15–30 h; Leu and Liou, 2013), and so a day was added to the counts to determine the date of spawning. The recruits from 2004/2005 ranged in age from 197 days (approximately 5 months) to 264 days old (approximately 9 months). They were spawned in May, June and July, and typically at around the same time. The earliest spawning date recorded was the 10 May. The potential settlers from 2015 ranged in age from 18 to 25 days, and were all spawned between the end of December 2014 and the beginning of January 2015. Accordingly, the spawning season for *L. carponotatus* could be long, continuous or made up of multiple discreet spawning periods within a year.

The locations of the settlement marks on the otoliths of the recruits from 2004/2005 were noted. The pelagic larval duration (PLD) of each recruit was calculated as the number of days between spawning and settlement. The average PLD was 25 days ± 0.6 SE (range 22–28 days) and the ages of 35% of the potential settlers from 2015 fell within the observed range of PLD's. The dates between spawning and settlement (2004/2005 recruits) or between spawning and capture (2015 potential settlers) were taken as the dates the fish were in the plankton as larvae.

Survivor Specific Wind Analysis

We determined the wind conditions present during the periods when the surviving *L. carponotatus* caught from OTI were in the plankton. The wind conditions have been measured hourly at a weather station on Heron Island (HI; 23°26′24.00″S, 151°55′12.00″E; **Figure 1C**), which is less than 10 km from OTI, from February 1999. These data were provided by the Australian Government Bureau of Meteorology. The longshore and cross shelf wind velocities were respectively calculated as the velocity components parallel and perpendicular to the 200 m isobath east of the CBG, which was measured to be offset 30° counter clockwise from the north/south axis. The ratios between the sums of the positive and negative vector components in the cross shelf (from the WSW and from the ENE) and longshore (from the SSE and from the NNW) directions were calculated for the dates when the fish were in the plankton. Longshore winds from the SSE were present when the 2004/2005 cohort of recruits were in the plankton as larvae, and these winds had a balanced (near 50:50) cross shelf vector ratio. Cross shelf winds from the ENE, with a balanced longshore wind ratio, were present during the pelagic larval phases of the potential settlers from the 2015 cohort. The cross shelf and longshore vector wind ratios were also calculated over 25 day intervals starting on successive days, from 1 January 2000 to 31 December 2016, in the same manner as a running average. A 25 day interval was used because it was the average PLD of the *L. carponotatus* recruits in this study. The wind ratios over the intervals, therefore, represent the winds that would have been present during the pelagic phases of *L. carponotatus* larvae spawned on each successive day over the 18 year period. The rarity of the identified conditions was determined by counting the number of historic 25 day intervals with winds as or more balanced (ratios closer to 50:50) than the winds the fish in this study survived during their pelagic phases.

We hypothesized that the identified longshore winds with a balanced cross shelf component and the identified cross shelf winds with a balance longshore component would be favorable for recruitment as they were survived by successful recruits. Defining these conditions as favorable, we predicted that the recruitment of *L. carponotatus* to OTI could have been related to the prevalence favorable winds during the time of peak larval production. Kritzer (2004) found that the gonadosomatic indices of female *L. carponotatus* from the Palm and Lizard Island groups peaked in October, November and December. Additionally, Russell et al. (1977) found that the recruitment of juvenile reef fish from multiple taxa to OTI peaked in January and February, suggesting larval production peaked in December and January. Therefore, the production of *L. carponotatus* larvae probably peaks at OTI from October through to January. Of the identified winds with balanced cross shelf and longshore components, only the winds with a balanced longshore component occurred

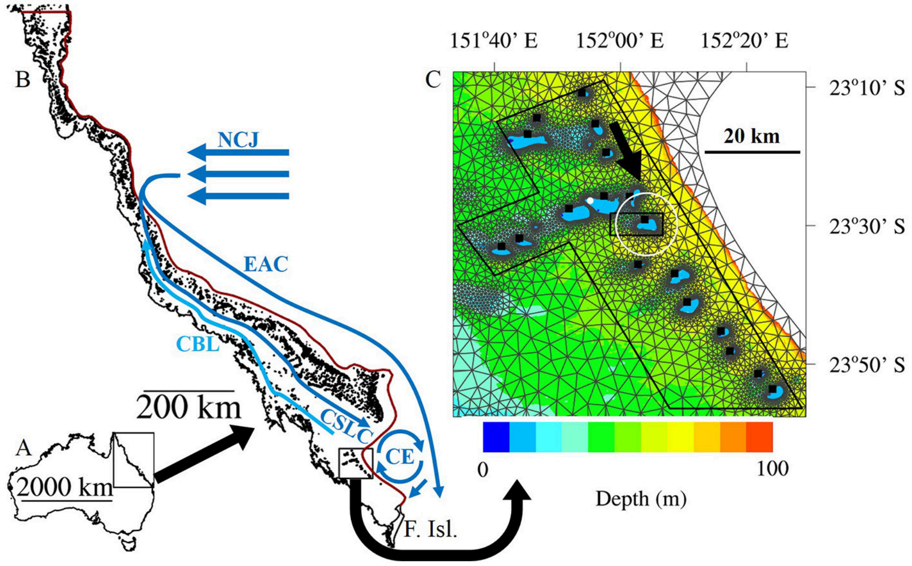

FIGURE 1 | The study region. **(A)** Australia. **(B)** The Great Barrier Reef (GBR). The broad scale oceanographic features of the southern GBR are shown including: The North Caledonian Jet (NCJ), the East Australian Current (EAC), the Coastal Boundary Layer (CBL), the Coral See Lagoonal Current (CSLC) and the Capricorn Eddy (CE). Adapted from Wolanski et al. (2013), and Mao and Luick (2014). The red line denotes the 200m isobath, which is also the open boundary of the model. The open boundary joins with the Queensland coast (closed boundary) at the tip of Australia to the north and at Fraser Island (F. Isl.) to the south. **(C)** A zoomed view of the Capricorn Bunker Group (CBG) overlayed with the SLIM mesh. *Lutjanus carponotatus* larvae were seeded from the locations marked by the black squares. When the larvae were active (B scenarios) they were programmed to swim to the SSE at a bearing of 155° (black arrow) unless they were within 5 km of One Tree Island (OTI; denoted by the white circle), where they were made to swim toward the center of OTI instead. The number of larvae remaining in the black irregular octagon were tracked through time to calculate the residence time of the CBG region. The number of potential settlers present around OTI were counted within the black rectangle at the end of the Pelagic Larval Duration. The white dot shows the location of Heron Island weather station. The bathymetry is only shown for depths less than 100 m.

during the period of peak production. The number of historic 25 day intervals with a balanced longshore component occurring in the peak production period (2000/2001–2015/2016) were correlated with the measured abundance of *L. carponotatus* recruits at OTI (2002–2017) to determine if the magnitude of recruitment was related to the prevalence of the winds. A Spearman's Correlation was performed because the data did not meet the Pearson's Correlation assumption of a bivariate normal distribution. A one-year time lag was applied as the recruits observed in any given year would have been produced in the preceding period of peak production. Further, biophysical modeling was carried out to determine the capacity for the identified winds to generate favorable currents when compared to seasonally dominant conditions, and to investigate the influence of the Capricorn Eddy (CE) and larval swimming behavior on recruitment.

Biophysical Modeling

The Second-generation Louvain-la-Neuve Ice-ocean Model (SLIM) was used to model the dispersion of *L. carponotatus* larvae from reefs in the CBG. SLIM has an unstructured grid which can be made finer in areas where a high resolution is required and coarser in open areas, prioritizing the allocation of computational power. Unstructured grids are particularly useful in coral reef systems (Lambrechts et al., 2008) as a high spatial resolution is required to avoid erasing small reefs and to accurately simulate the current shear distribution near reef edges (Wolanski et al., 1996). SLIM has been used to effectively model the hydrodynamics of the GBR system (e.g., Lambrechts et al., 2008; Delandmeter et al., 2017; Wildermann et al., 2017). The two-dimensional depth averaged version of SLIM was used in this study; this was valid because two-dimensional depth averaged models can realistically simulate observed currents in shallow, vertically well mixed water (Lambrechts et al., 2008). GBR shelf waters are generally shallow and vertically well mixed (Luick et al., 2007). Additionally, small scale three-dimensional modeling of the area around OTI showed that passive larvae released from OTI had similar dispersal patterns whether they were set to remain near the surface, at mid-depth or near the bottom (Critchell et al., 2015).

SLIM solves the shallow-water equations discretized in space with a second order discontinuous Galerkin finite element method and in time with a second order implicit Runge-Kutta method (Lambrechts et al., 2008). The hydrodynamic model has a time step of 10 min. The model domain encompassed the entire GBR with the open boundary following the 200 m isobath and the closed boundary following the Queensland coastline. The model mesh was made up of nearly 26,000 triangles, which ranged in size from less than 300 m near reefs to more than 20 km in open water (**Figure 1B**). The bathymetry data used in the model for areas outside of the CBG were derived from Geoscience Australia's Australian Bathymetry and Topography 2005 data set which has an ∼250 m resolution (Webster and Petkovic, 2005). The data for the CBG area were derived from Project 3DGBR data which has a 100 m resolution (Beaman, 2010). The model was forced at the open boundary (**Figure 1B**) with tides, the inflow of the North Caledonian Jet (NCJ) from the Coral Sea and the CE (some scenarios; **Table 1**). It was also forced with wind via a spatially uniform vector field applied over the entire domain.

The tidal conditions at OTI were predicted using AusTide 2015 version 1.10.1 and approximated with a synthetic semidiurnal tide with an amplitude of 1 m and a period of 12 h for use in the model. The magnitude and latitude of the NCJ inflow into the GBR system from the Coral Sea are largely unknown (Ganachaud et al., 2014). The NCJ was simulated as a 1.5×10^6 m^3 s^{-1} inflow between 15°54′36″ S and 17°43′12″ S following Andutta et al. (2011). The CE periodically forms off the continental shelf, to the east of the CBG. While the conditions preceding the formation of the eddy have been described (Mao and Luick, 2014), the frequency of formation and the magnitude of the resulting cyclonic currents are largely unknown. In scenarios 2 and 4, the CE was modeled as a 0.3×10^6 m^3 s^{-1} inflow from the open boundary north of Fraser Island and an outflow of equal magnitude added to the Coral See Lagoonal Current (**Figure 1B**).

The yearly average wind measured at Heron Island weather station from 1999 to 2013 was 6.2 m s^{-1} ± 2.7 SD and the prevailing wind direction was 119.9°. These average conditions were imposed as a constant wind in the average wind model runs (all 1 and 2 scenarios). In the strong wind runs (all 3 and 4 scenarios), a constant wind was still forced from the prevailing direction, but the velocity imposed was 1.5 times average (9.35 m s^{-1}). All combinations of constant wind (average or strong wind from the prevailing direction) and CE activity were modeled in scenarios 1–4 to predict the influence of physical conditions on *L. carponotatus* recruitment to OTI.

The longshore SSE and cross shelf ENE wind conditions present during the pelagic phases of the fish caught at OTI were also modeled to determine if they would generate currents conducive to the recruitment of *L. carponotatus* to OTI. These conditions were imposed as spatially constant, but temporally variable. For the 2004/2005 cohort, winds from the pelagic phases of fish that survived the SSE winds with the most balanced (cross shelf vector wind ratio closest to 50:50; scenario 5, SSE 1) and least balanced (ratio farthest from 50:50; scenario 6, SSE 2) cross shelf components were used. The fish in the 2015 cohort were all spawned within 8 days of each other so they experienced very similar conditions. Accordingly, a fish from this cohort was randomly chosen, and the ENE winds present during its pelagic phase were modeled (scenario 7, ENE). The output of the hydrodynamic model was saved every 30 min and coupled with the advection-dispersion model.

L. carponotatus larvae were seeded as particles in the advection-dispersion model. Although there are no data on the sources of *L. carponotatus* recruits to OTI, reefs in the CBG are a likely source. The potential for successful larval dispersal (dispersal kernels) tends to decrease with distance from the natal reef (Jones, 2015; Williamson et al., 2016). Further, Williamson et al. (2016) conducted a genetic parentage analysis to investigate patterns of connectivity in populations of two coral trout species, *Plectropomus maculatus* and *Plectropomus leopardus*, in the southern GBR. The PLD of both species was 26 days ± 2 SD, comparable to the 25 days ± 2 SD reported for *L. carponotatus* in this study. Samples were taken from reefs in the CBG, the

TABLE 1 | Modeled scenarios and results.

Scenario No.	Wind	CE present?	Behavior	CBG res time (days; avg ± SE)	# settlers (avg ± SE)	# settlers rank	% SS (avg ± SE)	% returned (avg ± SE)
1A	Average ($6.2\,\mathrm{m\,s^{-1}}$ from 119.9°)	No	Passive	18.3 ± 0.2	136.7 ± 8.4	4P	7.8 ± 0.3	1.1 ± <0.1
1B	Average	No	Swimming	23.2 ± 2.1	793.3 ± 15.2	7S	9.0 ± 0.7	7.2 ± 0.6
2A	Average	Yes	Passive	8.9 ± <0.1	56.3 ± 3.3	5P	1.8 ± 0.1	0.1 ± <0.01
2B	Average	Yes	Swimming	8.9 ± <0.1	1,589.0 ± 42.6	4S	0.4 ± 0.1	0.7 ± 0.2
3A	Strong ($9.4\,\mathrm{m\,s^{-1}}$ from 119.9)	No	Passive	11.9 ± <0.1	36.7 ± 3.2	6P	4.3 ± 1.3	0.2 ± 0.1
3B	Strong	No	Swimming	12.0 ± 0.1	826.3 ± 9.8	6S	4.4 ± 0.4	3.7 ± 0.3
4A	Strong	Yes	Passive	5.7 ± <0.1	36.3 ± 0.9	7P	17.3 ± 2.0	0.6 ± 0.1
4B	Strong	Yes	Swimming	5.7 ± <0.1	870.0 ± 11.0	5S	16.2 ± 0.6	14.1 ± 0.5
5A	SSE 1	No	Passive	22.9 ± <0.1	215.7 ± 11.3	1P	5.1 ± 0.4	1.1 ± 0.1
5B	SSE 1	No	Swimming	26.8 ± 0.1	2,848.0 ± 25.5	2S	6.3 ± 0.2	18.1 ± 0.4
6A	SSE 2	No	Passive	24.8 ± 0.1	189.0 ± 3.2	2P	9.2 ± 1.3	1.7 ± 0.2
6B	SSE 2	No	Swimming	>27 days	3,006.0 ± 19.2	1S	9.0 ± 0.3	26.9 ± 0.6
7A	ENE	No	Passive	>27 days	157.3 ± 4.6	3P	2.1 ± 0.7	0.3 ± 0.1
7B	ENE	No	Swimming	>27 days	2,681.0 ± 25.4	3S	3.0 ± 0.2	8.0 ± 0.6

*Shown are: the wind forcing; the status of the Capricorn Eddy (CE); the programmed behavior of the Lutjanus carponotatus larvae; the residence time of the Capricorn Bunker Group (CBG res time); the number of potential settlers present around One Tree Island (OTI) after 25 days, at the end of the Pelagic Larval Duration (PLD), counted from all 18,000 larvae seeded from the CBG (**Figure 1C**; # settlers); the ranking of scenarios by the # settlers, separated into scenarios with Passive (P) and Swimming (S) larvae; the Self-Seeding (SS) rate, calculated as the percentage of the # settlers that originated from OTI (% SS); the percentage of the 1000 larvae seeded from OTI that returned to OTI as potential settlers (% returned). The CBG res time was recorded as >27 days if it was not reached by the end of the model run.*

Keppel Islands (~100 km from the CBG) and the Percy Island Group (~250 km from the CBG). *P. leopardus* were substantially more abundant in the CBG than *P. maculatus*, comprising 81% of all coral trout sightings in the region. However, *P. maculatus* were more abundant than *P. leopardus* in the other study regions, comprising 99 and 84% of coral trout sightings in the Keppel Islands and the Percy Island Group respectively. A large majority (74%) of the parentage assigned *P. leopardus* recruits to the CBG were spawned from reefs in the CBG. Despite the comparable rarity of *P. maculatus* in the CBG, a large proportion (44%) of the parentage assigned *P. maculatus* recruits to the CBG also came from within the region. Further, late stage *P. leopardus* larvae did not swim as strongly as *L. carponotatus* larvae when tested in a flume tank (Fisher et al., 2005), suggesting *L. carponotatus* have a greater capacity to limit their dispersal. Due to a lack of available data, we made the simplifying assumptions that recruits to OTI would come from OTI and other reefs in the CBG, and that the adults from these reefs would have the same reproductive capacity. Accordingly, 1,000 larvae per reef were seeded from 18 reefs in the CBG, including OTI (18,000 larvae in total; **Figure 1C**). We made the further simplifying assumption that larvae advected outside of the model domain would not be able to return, even though mesoscale eddy activity has been associated with the delivery of fish larvae to reefal waters (e.g., Sponaugle et al., 2005) and the CE lies just outside of the model domain (see Discussion section The Capricorn Eddy). The effect of sub-grid scale processes on diffusion were simulated with a horizontal diffusion coefficient. While the exact value of the coefficient is unknown, 5 $\mathrm{m^2\ s^{-1}}$ is realistic (Spagnol et al., 2002; Wolanski and Kingsford, 2014) and was therefore used in this study. The use of a two-dimensional model necessitated the assumption that larvae were vertically well mixed in the water column.

Larvae were either passive or active, depending on the model scenario. The swimming speed of the active larvae was set to change through time as they developed, following Wolanski and Kingsford (2014). Larvae were set to begin swimming when they reached post-flexion. The swimming speed then increased linearly to the maximum sustainable swimming speed, which was maintained up until the end of the PLD. Thereafter, the swimming speed was reduced to zero because the larvae were assumed to be exhausted. The swimming speed was changed through time as follows:

$$U_{swim} = \begin{cases} 0, & t < T_{post-flexion} \\ \frac{U_{max} \times \left(t - T_{post-flexion}\right)}{T_{max} - T_{post-flexion}}, & T_{post-flexion} \le t < T_{max} \\ U_{max}, & T_{max} \le t < PLD \\ 0, & t \ge PLD \end{cases} \tag{1}$$

where t was the time and U_{swim} was the swimming speed of the larvae. The maximum sustainable swimming speed, U_{max}, was set to 26 $\mathrm{cm\ s^{-1}}$, which is half of the critical swimming speed for late stage *L. carponotatus* larvae (52 $\mathrm{cm\ s^{-1}}$; Fisher et al., 2005).

Half of the critical swimming speed is a good approximation of U_{max} (Fisher and Wilson, 2004) and a U_{max} of 26 cm s^{-1} is within the range of values calculated for lutjanids (18–29 cm s^{-1}) by Fisher and Bellwood (2002). $T_{post-flexion}$ was the time taken for the larvae to develop to post-flexion. Eggs were assumed to hatch 1 day after spawning (Leu and Liou, 2013). Notochord flexion, which marks the beginning of the post-flexion phase, was assumed to be complete 16 days after hatching, which is within the range of values recorded for lutjanid species (16 to 18 days; Clarke et al., 1997). $T_{post-flexion}$ was therefore set to 17 days. T_{max} was the time taken for the larvae to be able to swim at U_{max}. As mentioned the average PLD calculated for the *L. carponotatus* recruits caught at OTI was 25 days ± 0.6 SE. T_{max} was set to 21 days, 4 days before the end of the PLD (Wolanski and Kingsford, 2014).

The swimming direction of the active larvae was determined from the prescribed behaviors. Larvae were made to swim to the SSE at a bearing of 155°. A strong SSE directional swimming response was reported for pre-settlement larvae and early settlers of the cardinal fish species *Ostorhinchus doederleini* caught and tested near OTI (Mouritsen et al., 2013). Mouritsen et al. (2013) suggested that the response evolved to counteract the prevailing NNW current. It was demonstrated that the *O. doederleini* larvae were navigating using a sun compass mechanism (Mouritsen et al., 2013) and sun compass orientation has also been documented in other coral reef fish species (e.g., Leis and Carson-Ewart, 2003; Berenshtein et al., 2014). Bottesch et al. (2016) demonstrated that newly settled *O. doederleini* at OTI can also orient their swimming to the SE at night via a magnetic compass mechanism. In this study, it was assumed that *L. carponotatus* spawned from reefs in the CBG (which are affected by the same prevailing NNW current as OTI) would have a strong SSE directional swimming response like *O. doederleini*.

When larvae got to within 5 km of OTI, they were made to swim toward the center of OTI, rather than to the SSE. This represents the chemotaxis driven orientation documented in the larvae of many coral reef fish species, where they can swim to reefs by discriminating between water with a reef odor and oceanic water (e.g., Paris et al., 2013). Wolanski and Kingsford (2014) simulated the odor plume from OTI and found it extended several kilometers from the reef.

For each combination of physical forcings, larvae were modeled as passive in the "A" scenarios and as actively swimming in the "B" scenarios to determine the influence of swimming behavior on recruitment. All scenarios were run for 27 days, 2 days longer than the average PLD, and are summarized in **Table 1**. Three replicate runs were conducted per scenario to account for the inherent variability in the model.

Quantifying the Modeling Results

The residence time (the average time a "tracer" will remain in a system; Black et al., 1991) of the CBG was calculated to determine the capacity for retention within the CBG for each of the modeled scenarios (**Figure 1C**). It was calculated as the time taken for the concentration of larvae within the CBG to fall to 1/e (∼0.37) of its original value, following Prandle (1984) and Choi and Lee (2004).

The number of larvae near OTI at the end of the PLD (25 days) were counted for each of the modeled scenarios to estimate the number of potential settlers (**Figure 1C**). It was assumed that the potential settlers would be able to hear the ambient noise from OTI if they were within 1 km of the reef (Mann et al., 2007). The number of potential settlers were therefore counted within a rectangular capture box, with bounds located 1 km to the north, south and east of OTI. Larvae were counted at high tide, so the box was extended out to the west by 5 km to account for the larvae that would have been transported into the capture area with the tidal excursion over 6 h as the tide went out. The capture distances used are conservative given Radford et al. (2011) detected reef noise 5 km from a reef and larvae can likely smell OTI from several kilometers away (Wolanski and Kingsford, 2014). The Self-Seeding rate (% SS) was subsequently calculated as the percentage of the total number of settlers counted around OTI that had originally been seeded from OTI. The return rate (% return) was calculated at the percentage of the 1,000 larvae seeded from OTI that returned to OTI. Expressed mathematically:

$$\%\ \mathrm{SS} = \frac{n_{OTI}}{n_{TTL}} \times 100 \tag{2}$$

$$\%\ return = \frac{n_{OTI}}{1000} \times 100 \tag{3}$$

where n_{TTL} was the total number of potential settlers counted around OTI and n_{OTI} was the subset of counted potential settlers that had originally been seeded from OTI.

Model Validation

The currents simulated by SLIM were an accurate reproduction of the currents in the CBG region. The hydrodynamic model was validated by comparing the outputs to drifter data from Mantovanelli et al. (2012) and depth averaged Acoustic Doppler Current Profiler (ADCP) data (averaged from below the depth affected by side lobe interference) from the Integrated Marine Observing System (IMOS) as follows. Mantovanelli et al. (2012) released 4 drifters to the south of Heron Island on 25 April 2010 and left them to drift for 20 days, until 15 May 2010. One of the drifters ran aground on the 03 May 2010 and was redeployed for a further 27 days, from 15 May 2010 to 11 June 2010. The winds present over the entire 47 day period (average velocity = 5.5 m s^{-1} ± 2.4 SD, prevailing direction = 160.8°) most closely matched the winds modeled in scenario 6 (SSE 2; average velocity = 6.3 m s^{-1} ± 3.0 SD, prevailing direction = 160.0°). Of all the seed locations used in the modeling, the location on the lee side of Lamont Reef was the closest to the initial release point of the drifters. One thousand passive larvae were seeded from Lamont Reef in scenario 6 A; the dispersal of the larval plume at the end of the 27 day run approximately matched the dispersal of the drifters (**Figure 2A**). Nearly half of the larvae remaining in the model domain at the end of the run were within the area bound by the paths the drifters traveled (448 of 939 remaining larvae, 47.7%). The northernmost distance a larva traveled from Lamont Reef approached the northernmost distance reached by a drifter. Further, the median longshore and cross shelf current velocities simulated in scenario 7, which was forced with wind from the 01 January 2015 to 25 January 2015, closely matched the median depth averaged current velocities measured at the Heron Island South and One Tree East moorings in the same period (**Figure 2B**). The simulated current ranges also approximately matched the measured ranges.

Finally, to validate the simulation of the CE, we compared the currents simulated in scenario 2, which was forced with the CE and average wind, with ADCP measurements taken during identified eddy events. Weeks et al. (2010) identified an eddy event which lasted for a least 9 days, from 27 September 2008 to 6 October 2008. Mao and Luick (2014) identified additional eddy events; one lasted for at least 6 days, from 1 May 2010 to 7 May 2010, and a second lasted for at least 2 days, from 14 July 2010 to 16 July 2010. The average velocities simulated in SLIM at the mooring locations (0.25 m–0.45 m s^{-1}; **Figure 2C**) were within the range of velocities measured during the identified eddy events (0.17–0.46 m s^{-1}). The current directions predicted in SLIM aligned well with the directions measured at the Capricorn Channel and One Tree East moorings during the May 2010 eddy event. The current directions predicted at the Heron Island North and Heron Island South moorings did not align with any identified event; however, the current directions measured at these mooring varied greatly between events.

RESULTS

The Long-Term Abundance of *Lutjanus carpontatus* at One Tree Island

The number of recruits observed within the lagoon at One Tree Island (OTI) varied greatly among years over the 23 year period, from 1995 to 2017 (**Figure 3A**). Either zero or very few *Lutjanus carponotatus* recruits were observed in edge or center habitats from 1995 to 2002 and from 2013 to 2015. After 2002, four peaks (*sensu* average > 0.3 recruits per 125 m^2) in recruitment were recorded in the lagoon habitats. The greatest numbers of recruits were observed in 2011. The average abundance recorded in the lagoon habitats in this year was 1.7 times greater than the averages recorded for the next highest peaks in recruitment,

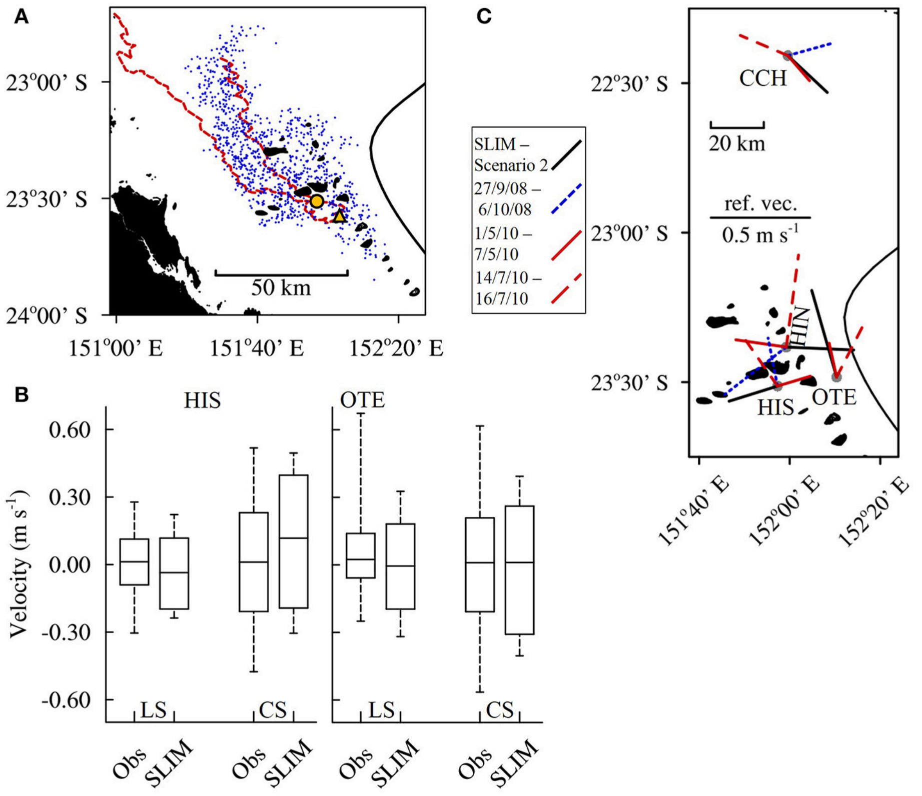

FIGURE 2 | SLIM validation. **(A)** The maximum extents (red dashed line) traveled by the 4 drifters Mantovanelli et al. (2012) released south of Heron Island (yellow circle) over the 20–27 days they were left adrift. The paths are superimposed on top of a plume of passive larvae (blue dots) 27 days after they were seeded from Lamont reef (yellow triangle) in model scenario 6. **(B)** The LongShore (LS) and Cross Shelf (CS) currents that were simulated (SLIM) at mooring locations Heron Island South (HIS) and One Tree East (OTE) in scenario 7, which was forced with wind from 01 January 2015 to 25 January 2015. These data are compared to the depth averaged currents that were measured (obs) at the moorings over the same period. The locations of the moorings are shown in **(C)**. **(C)** The currents simulated in scenario 2 (solid black line), where the Capricorn Eddy was modeled as present, in combination with wind of average strength (6.2 m s^{-1}) from the prevailing direction (119.9°), compared to the depth averaged currents measured at moorings during identified eddy events (blue and red lines). The lengths of the lines indicate the mean current velocities and the line orientations indicate the prevailing directions the currents traveled away from the mooring locations (gray dots). Data from the Capricorn CHannel (CCH), Heron Island North (HIN), HIS and OTE moorings are shown.

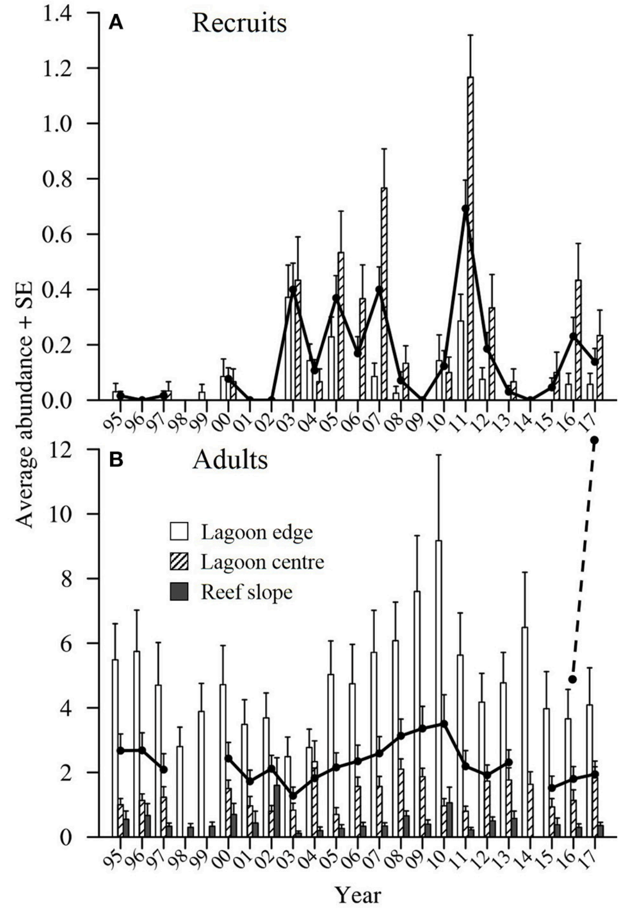

FIGURE 3 | The average abundance of **(A)** *Lutjanus carponotatus recruits* (<150 mm standard length; SL) and **(B)** *L. carponotatus* adults (>200 mm SL) per 125 m^2 ± SE recorded in lagoon center, lagoon edge and reef slope habitats at OTI in January/February of each year (six or seven sites per habitat and $n = 5$ transects). The black lines show the overall average abundance. The overall average recruit abundance does not include data from the reef slope habitat as no recruits were observed in this habitat. The overall averages have not been shown for years when all relevant habitats were not sampled. A one-year time lag was applied when the abundance of adults was correlated with the abundance of recruits, as indicated by the dashed line.

which occurred in 2003 and 2007. Greater numbers of recruits were generally observed at the lagoon center habitat than the lagoon edge.

The average abundance of *L. carponotatus* adults recorded in the lagoon was relatively high in all years, although the numbers observed fluctuated among years (**Figure 3B**). The average abundance among all habitats peaked at 3.50 adults per 125 m^2 ± 0.9 SE (used as the measure of variance thereafter unless otherwise specified) in 2010. Adult abundance increased from 2004 to 2010, after sustained recruitment from 2003 to 2007. It also increased from 2012 to 2014 following the largest recruitment peak in 2011. The abundance of adults was relatively stable from 2015 to 2017, following a recruitment failure in 2014 and moderate to low recruitment thereafter. The average abundance of recruits did not correlate with the average abundance of adults (used as a proxy for spawner biomass) recorded in the previous year [Spearman's rank correlation, $r_s = -0.13$, $z_{(2)} = -0.55$, $p > 0.05$, $n = 18$].

Wind Conditions Present During the Larval Period

Wind in the CBG region typically blew from the ESE (117.8° from true north) with an average velocity of 6.1 m s^{-1} ± 2.6 SD (**Table 2**). When the recruits from the 2004/2005 cohort were in the plankton as larvae, the wind predominantly blew longshore, from the SSE (155.0°) at a near average velocity (6.9 m s^{-1} ± 0.7 SD; **Figures 4A,B**). At the end of the recruits Pelagic Larval Duration's (PLD's), the cumulative sum of the wind's cross shelf component neared zero as the component alternated in direction, blowing from the ENE (42.4% ± 7.7 SD) and the WSW (57.6% ± 7.7 SD). These sums were much more balanced (cross shelf cumulative sum ratio closer to 50:50 ENE:WSW) than in an average 25 day period (78.6% ± 21.5 SD from the ENE and 21.4% ± 21.5 SD from the WSW). Winds with cross shelf components as or more balanced than the observed SSE winds occurred on 72 PLD length intervals ±7 in a year on average. Winds with balanced cross shelf components were most common in May, June, and July (**Figure 5**), when the recruits from the 2004/2005 cohort were spawned.

The wind predominantly blew across the shelf, from the ENE (64.6°), at below average velocity (5.4 m s^{-1} ± 0.1 SD), when the pre-settlement fish from the 2015 cohort were in the plankton as larvae (**Figure 4C**). The cumulative sum of the wind's longshore component neared zero over the period when the fish were in the plankton, as the component alternated in direction, blowing from the NNW (46.6% ± 2.7 SD) and the SSE (53.4% ± 2.7). These sums were much more balanced (longshore cumulative sum ratio closer to 50:50 NNW:SSE transport) than in an average 25 day period (22.2% ± 19.9 from the NNW and 77.8% ± 19.9 from the SSE). Winds with longshore components as or more balanced than the observed ENE winds were rarer than balanced cross shelf winds, occurring on only 29 PLD length intervals ± 4 in a year on average. They were most common from August to January, when winds with balanced cross shelf components were largely absent (**Figure 5**). This period includes the months when the production of *L. carponotatus* larvae is likely greatest, from October to January. The prevalence of winds with a balanced longshore component during this period of peak production was positively correlated with the abundance of recruits observed in the following year [Spearman's rank correlation, $r_s = 0.51$, $z_{(2)} = 1.97$, $p < 0.05$, $n = 15$; **Figure 6**].

Retention Under Modeled Conditions

The wind conditions present during the pelagic phases of the *L. carponotatus* caught at OTI in both the 2004/2005 and the 2015 cohorts drove currents that minimized the expatriation of larvae from the Capricorn Bunker Group (CBG). The SSE winds present during the pelagic phases of the recruits from the 2004/2005 cohort partly advected the plume of passive larvae longshore, to the NNW, but induced little net cross shelf transport (scenarios 5A and 6A; **Figures 7E,F**). The plume, therefore, remained concentrated in the CBG for the duration of the 27 day run;

TABLE 2 | Wind metrics for: Row (1) historic, successive 25 day (average Pelagic Larval Duration length) intervals from 1 January 2000 to 31 December 2016 (long term), Row (2) the winds present during the planktonic phases of the recruits from the 2004/2005 cohort, Row (3) the winds present during the planktonic phases of the potential settlers from the 2015 cohort.

			Cross Shelf Axis		**Longshore Axis**	
Wind	**Velocity (m s^{-1}; avg. ± SD)**	**Direction**	**%CS from ENE (avg. ± SD)**	**% CS from WSW (avg. ± SD)**	**% CS from NNW (avg. ± SD)**	**% CS from SSE (avg. ± SD)**
Long term (2000–2016)	6.1 ± 2.6	117.8°; ESE	78.6 ± 21.5	21.4 ± 21.5	22.2 ± 19.9	77.8 ± 19.9
2004/2005 cohort	6.9 ± 0.7	155.0°; SSE	42.4 ± 7.7	57.6 ± 7.7	8.2 ± 5.2	91.8 ± 5.2
2015 cohort	5.4 ± 0.1	64.6°; ENE	93.4 ± 0.6	6.6 ± 0.6	46.6 ± 2.7	53.4 ± 2.7

Shown are: the average wind velocities, prevailing directions and the average contributions to the cumulative sums of the cross shelf (from the WSW and from the ENE) and longshore wind velocities (from the SSE and from the NNW) from the positive and negative directions, expressed as percentages of the total cumulative sum. Separate calculations were made for each axis.

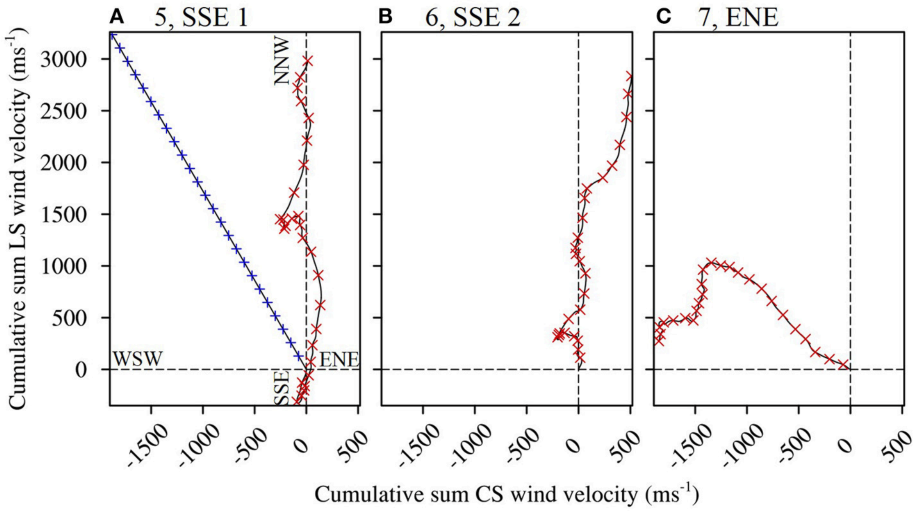

FIGURE 4 | Progressive vector diagrams of the winds present during the planktonic larval phases of select fish caught from One Tree Island. Trajectories to the right of the Y axis indicate a net Cross Shelf (CS) velocity component from the WSW, and trajectories to the left of the axis indicate a net ENE component. Trajectories above the X axis indicate a net LongShore (LS) velocity component from the SSE, and trajectories below the axis indicate a net NNW component. The winds were forced in the modeling scenarios as follows. **(A)** Scenario 5, LS winds predominantly from the SSE with the most balanced cross shelf (CS) component (red cross symbols). Scenarios 1 and 2, with wind of average speed (6.2 m s^{-1}) from the prevailing direction (from 119.9°; blue plus symbols). **(B)** Scenario 6, LS winds predominantly from the SSE with the least balanced CS component (a greater WSW component). **(C)** Scenario 7, CS winds predominantly from the ENE with a balanced LS component.

the residence time of the CBG in these scenarios (22.9 days ± <0.1 to 24.8 days ± 0.1; **Figure 8C**, **Table 1**) approached the average PLD of the *L. carponotatus* recruits from this study of 25 days ± 0.6. Analogously, the plume of passive larvae was partly advected across the shelf, to the WSW, by the ENE winds present during the pelagic phases of the potential settlers from the 2015 cohort (scenario 7A; **Figure 7G**). These winds induced little longshore transport and so the plume remained concentrated in the CBG; the residence time of the CBG in this scenario (>27 days; **Figure 8C**) exceeded the average *L. carponotatus* PLD. The plume of passive larvae also remained relatively concentrated in the CBG under winds of average strength from the prevailing ESE direction and no Capricorn Eddy (CE; scenario 1A; **Figure 7A**). The plume was partly advected to the WNW, and the residence time in this scenario (18.3 days ± 0.2; **Figure 8A**) was at least 4 days shorter than the times recorded under the SSE and ENE winds real larvae had survived. Strong wind conditions in the prevailing direction quickly advected passive larvae to the NW, far away from the CBG (scenarios 3A and 4A; **Figures 7C,D**). The CE also reduced retention in the CBG by expatriating large numbers of passive larvae eastward into oceanic waters over the shelf slope. This was consistent when the CE was modeled in combination with average winds (scenario 2A; **Figure 7B**) and with strong winds (scenario 4A; **Figure 7D**). Accordingly, the residence times of the CBG recorded in these scenarios (5.7 days ± <0.1 to 12.0 days ± 0.1; **Figures 8A,B**) were days to weeks shorter than the residence times recorded under the survivor specific wind conditions, or under average winds and no CE.

The impact of larval swimming behavior on the dispersal of the larval plume, and the corresponding residence time of the CBG, depended on the model scenario. In the scenarios where the plume of passive larvae remained relatively concentrated in the

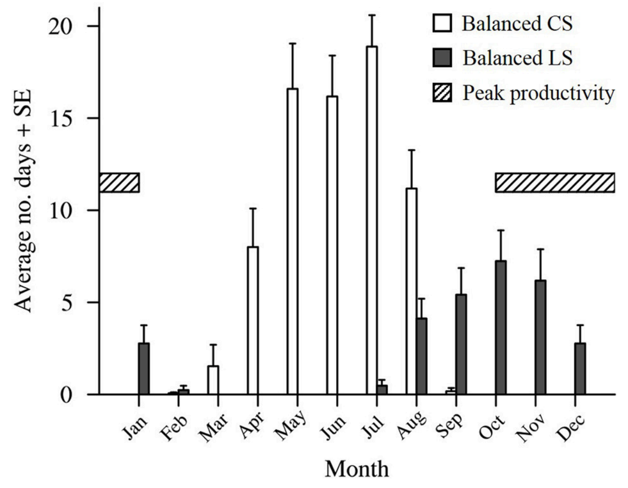

FIGURE 5 | The average number of historic 25 day (average Pelagic Larval Duration length) intervals starting in each month (2000–2016) that had winds with LongShore (LS) and Cross Shelf (CS) components as or more balanced than the winds present during the planktonic larval phases of the fish caught from One Tree Island. The striped section indicates the period of peak *Lutjanus carponotatus* larval production.

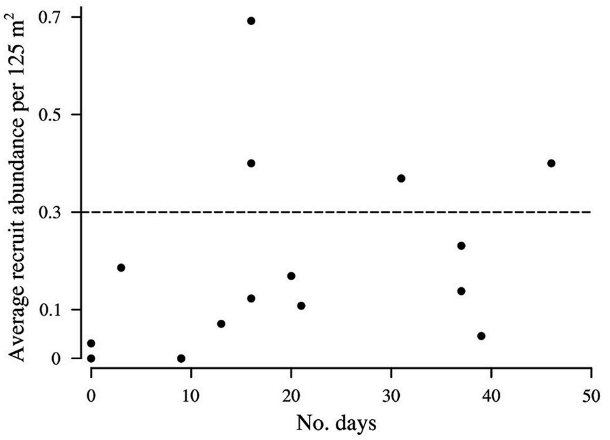

FIGURE 6 | The average number of *Lutjanus Carponotatus* recruits observed at OTI in the lagoon habitats per 125 m^2 (2002–2017) in relation to the number of historic 25 day (average Pelagic Larval Duration length) intervals with a balanced longshore component present in the period of peak *L. carponotatus* larval production (2000/2001 to 2015/2016). Recruitment peaks occurred where the average abundance exceeded 0.3 recruits per 125 m^2, as marked by the dashed line. The SE's of the average abundances are shown in **Figure 3**.

CBG (scenarios 1A, 5A, 6A, and 7A), the inclusion of swimming behavior increased the residence time by several days (**Table 1**). For example, when the model was forced with the longshore SSE winds that had the least balanced cross shelf component, and no CE (scenarios 6A and 6B), the inclusion of swimming behavior reduced the NNW movement of the larval plume (**Figures 7F,H**) and increased the residence time of larvae in the CBG from 24.8 days ± 0.1 to >27 days. Swimming behavior had little effect on the residence time when the model was forced with strong winds or the CE, which both advected the larval plume away from the CBG. For example, when the CE was modeled in combination with average winds (scenarios 2A and 2B), the residence time did not measurably increase from 8.9 days ± <0.1 when swimming behavior was included.

At a smaller spatial scale, when the larvae were set to be passive (A scenarios), the highest numbers of potential settlers were recorded around OTI in the scenarios forced with the real winds survived by *L. carponotatus* during their pelagic phase's (scenarios 5A, 6A and 7A; # settlers rank 1P to 3P; 157.3 settlers ± 4.6–215.7 settlers ± 11.3; **Figure 9A**, **Table 1**). Slightly lesser numbers were recorded under average winds and no CE (scenario 1A; # settlers rank 4P; 136.7 settlers ± 8.4). Only around one third of the number of potential settlers recorded in the survivor specific conditions were counted in the model scenarios that included strong winds and/or the CE (scenarios 2A, 3A, and 4A; # settlers rank 5P to 7P; 36.3 settlers ± 0.9 to 56.3 settlers ± 3.3).

When swimming behavior was included (B scenarios), order of magnitude increases in the number of potential settlers were predicted for all the modeled physical conditions (**Figure 9B**). For example, in scenario 5, which was forced with longshore winds from the SSE, the number of potential settlers increased by 13 times, from 215.7 settlers ± 11.3–2848.0 settlers ± 25.5 when larval swimming was included. The greatest numbers of settlers were again counted in the scenarios forced with the real winds survived by *L. carponotatus* from OTI during their pelagic phase (scenarios 5B, 6B, and 7B; # settlers rank 1S to 3S; 2681.0 settlers ± 25.4 to 3006.0 settlers ± 19.2). In contrast to the results obtained for passive larvae, the next highest numbers of settlers were counted in the scenarios that included strong winds and/or the CE (scenarios 2B, 3B and 4B; # settlers rank 4S to 6S; 826.3 settlers ± 9.8–1589.0 settlers ± 42.6), which had one third to one half of the numbers of settlers recorded under the survivor specific wind conditions. Among the scenarios that included swimming, the lowest number of potential settlers were recorded in scenario 1B, which was forced with average winds and no CE (# settlers rank 7S; 793.3 settlers ± 15.2).

Additionally, including swimming behavior reduced the larval mortality from expatriation. The percentage of the original 1,000 larvae seeded from OTI that were present around OTI at the end of the PLD (% returned) increased when swimming behavior was included, and was substantial in some scenarios (**Table 1**). For example, the % return increased from 1.7% ± 0.2 under the longshore SSE winds with the least balanced cross shelf component, no CE and passive larvae (scenario 6A) to 26.9% ± 0.6 when the same oceanographic forcings were used, but the larvae were made to swim (scenario 6B).

Modeled Self-Seeding of One Tree Island

There was no clear pattern relating the Self-Seeding rate (% SS) at OTI to the modeled oceanographic conditions. For example, when the model was forced with winds of average strength from the prevailing direction and no CE, and larvae were made to swim (scenario 1B), the % SS was 9.0 % ± 0.7 (**Table 1**). When the CE was modeled as present, with the same wind and larval behavior (scenario 2B), the % SS decreased by an order of magnitude to 0.4

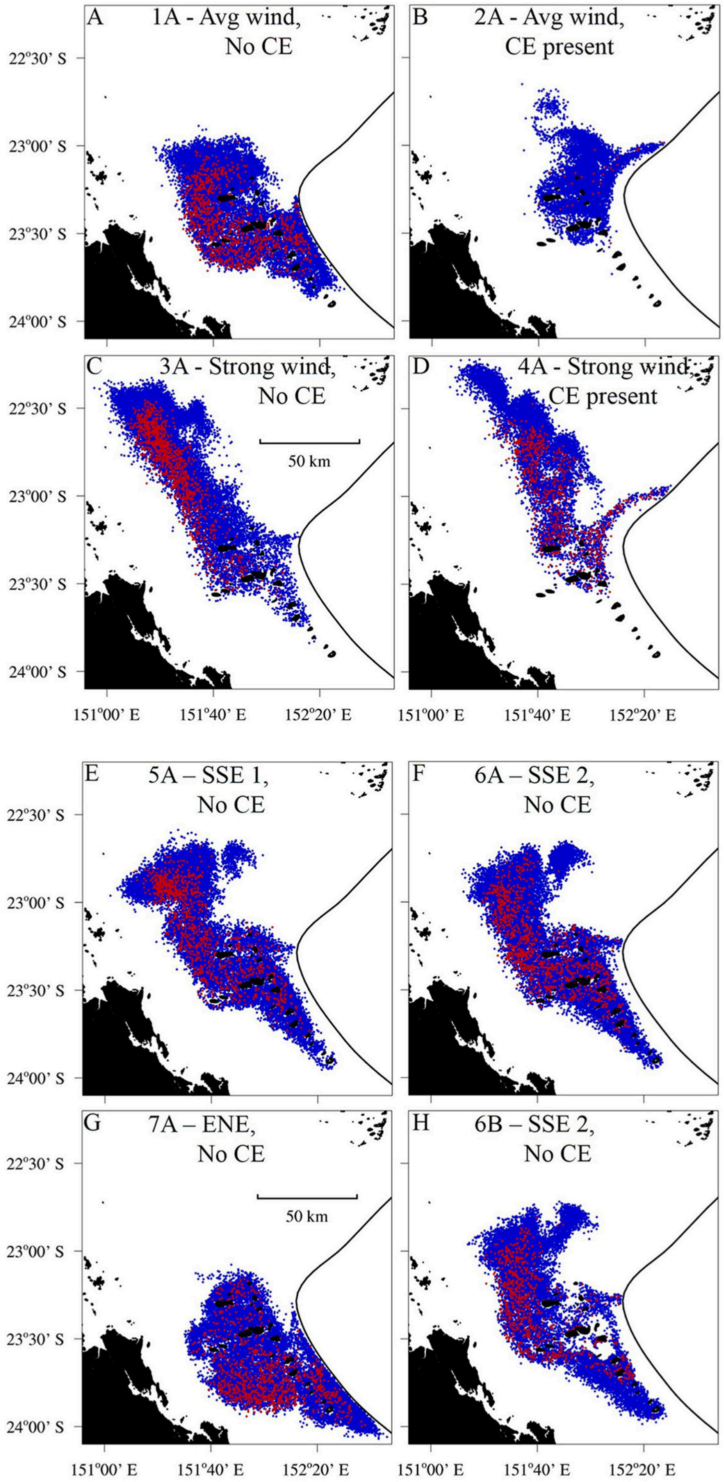

FIGURE 7 | The dispersion of the larval plume at the end of the Pelagic Larval Duration (PLD), 25 days after the larvae were seeded. The black line denotes the open boundary of the model which corresponds to the 200 m isobath. The red particles were seeded from One Tree Island (OTI) and the blue particles were seeded from other reefs in the Capricorn Bunker Group (**Figure 1C**). **(A–D)** Constant wind scenarios. **(A)** Wind of average strength (6.2 m s^{-1}) from the prevailing direction (119.9°), no Capricorn Eddy (CE) and passive larvae. **(B)** Average wind from the prevailing direction, the CE present and passive larvae. **(C)** Strong wind (1.5 times average) from the prevailing direction, no CE and passive larvae. **(D)** Strong wind from the prevailing direction, the CE present and passive larvae. **(E–G)** Alternating wind scenarios. **(E)** The LongShore SSE winds with the most balanced cross shelf (CS) component, no CE and passive larvae. **(F)** The LS SSE winds with the least balanced CS component (i.e., a stronger WSW component), no CE and passive larvae. **(G)** The CS winds with a balanced LS component, no CE and passive larvae. **(H)** The LS SSE winds with the least balanced CS component, no CE and swimming larvae.

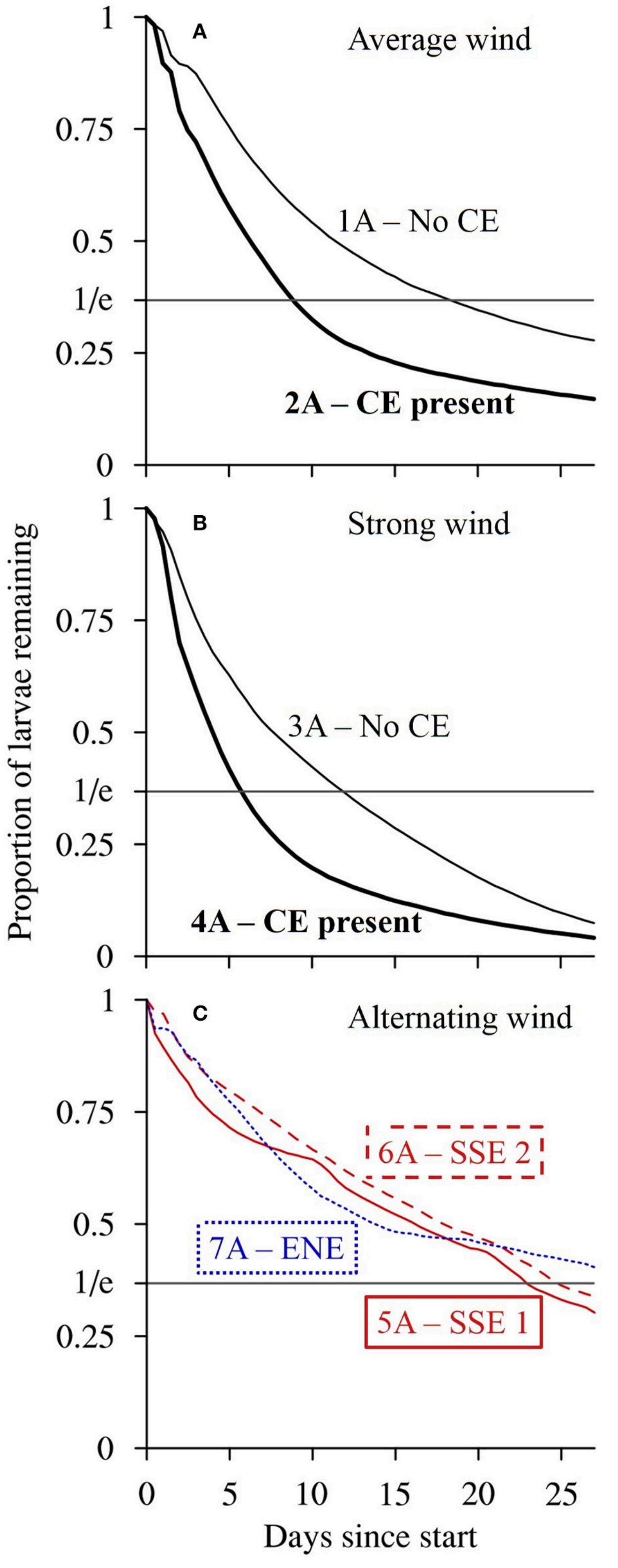

FIGURE 8 | The modeled proportion of passive larvae (A scenarios) seeded from reefs in the Capricorn Bunker Group (CBG, **Figure 1C**) remaining in the CBG through time up to the end of the 27-day model runs. The scenario

(Continued)

FIGURE 8 | numbers are shown. **(A)** Winds of average strength (6.2 m s^{-1}) from the prevailing direction (119.9°), with (bold) and without the Capricorn Eddy (CE). **(B)** Strong winds (1.5 times average) from the prevailing direction with (bold) and without the CE. **(C)** The LongShore (LS) SSE winds with balanced Cross Shelf (CS) components (red; most balanced = solid, least balanced = dashed) and the CS ENE winds with a balanced LS component (blue dotted) present during the planktonic larval phases of fish caught from OTI. The residence time is calculated as the time taken for the proportion remaining to fall to 1/e ~ 0.37.

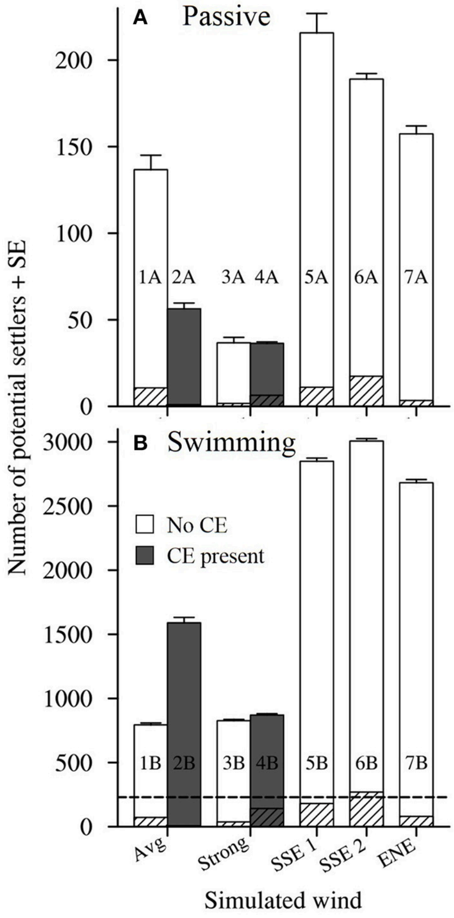

FIGURE 9 | The number of potential settlers seeded from reefs in the Capricorn Bunker Group (**Figure 1C**) that were present around One Tree Island at the end of the average Pelagic Larval Duration (PLD; 25 days ± 0.6 SE). **(A)** Passive larvae, A scenarios. **(B)** Swimming larvae, B scenarios. Runs with the Capricorn Eddy (CE) are shown in gray and runs without the CE are shown in white. The striped sections indicate the number of settlers counted that originated from OTI. The panes have different Y-axes, with the maximum extent of the Y-axis in A shown by the dotted line in **(B)**.

% ± 0.1, the lowest modeled % SS. Contrastingly, the inclusion of the CE increased the % SS that was projected with swimming larvae under strong winds, from 4.4% ± 0.4 (scenario 3B) to 16.2 % ± 0.6 (scenario 4B). The highest modeled % SS was 17.3% ± 2.0, and it was recorded in scenario 4A, with strong winds from the prevailing direction, the CE present and passive larvae. The inclusion of swimming behavior had little effect on the % SS in all scenarios. For example, the % SS only differed by 1.2% in the scenarios with and without swimming, when the model was forced with the longshore SSE winds with the most balanced cross shelf component, and no CE (scenarios 5A and 5B).

DISCUSSION

Lutjanus carponotatus Population Dynamics

The abundance of adult *Lutjanus carponotatus* at One Tree Island (OTI) remained relatively high throughout the 23 years of sampling and did not vary as much as the abundance of recruits. Our observations of increases in adult abundance following recruitment events suggested that the size of the population of *L. carponotatus* at OTI was determined by the cumulation of a few "stored" strong pulses of recruitment. The recruitment limitation of populations can occur, where the size of an adult population varies with the level of recruitment, assuming post settlement mortality is density independent (Doherty, 1983; Victor, 1983, 1986). Our findings align with those of Kingsford (2009) who investigated the age structure of the *L. carponotatus* population at OTI in the years after the 2003 recruitment pulse, which broke an 8-year lull in recruitment. The cohort that recruited in 2003 made up a large proportion (40–50%) of the total population in the 2 years following the pulse (Kingsford, 2009).

The lack of a correlation between the abundance of adult *L. carponotatus* at OTI and the abundance of the recruits that they could have spawned suggests that, at the scale of OTI, there was a decoupling between spawner biomass and recruitment. Numerous factors can act between spawning and recruitment, obscuring the relationship between the biomass of spawners and the magnitude of recruitment (Jennings et al., 2001). An overview of some of the factors that can affect the abundance of recruits is provided in the next section of the discussion. The population of adult *L. carponotatus* at OTI may only make up a fraction of the total population of adults contributing offspring to the island, hindering our ability to identify a spawner-recruit relationship (Jennings et al., 2001). This idea is supported by the low levels of self-seeding projected for OTI as, if the potential for self-seeding is limited, most of the fish recruiting to OTI would have been spawned from other reefs. The self-seeding rate was calculated to be less than 17% among all the modeled scenarios. Comparatively, the percentage of self-seeding has been estimated to be as high as 60% in other reef fish populations (Jones et al., 1999; Almany et al., 2007). The projected low levels of self-seeding at OTI are probably related to the geography of the Capricorn Bunker Group (CBG). The potential for self-seeding in reef matrices has been linked to the "sticky water" effect, whereby the net currents within a matrix are reduced through the deflection of currents around reefs, facilitating the retention of larvae (Andutta et al., 2012). The strength of the effect is dependent on the density of the reef matrix (Andutta et al., 2012). The capacity for self-seeding is therefore limited at more isolated reefs like those in the CBG, including OTI (Wolanski and Kingsford, 2014).

The rate of self-seeding of *L. carponotatus* at OTI presented here was estimated using biophysical modeling. We used a two-dimensional, depth average model and restricted the geographic extent of the seed locations to the CBG. All models are subject to potential error and, while these choices were necessary and justified (see methods), they could have affected the modeled patterns of connectivity. Two dimensional models can only incorporate two-dimensional behaviors so our model could not include larval vertical migration, which can enhance retention near natal reefs (Paris and Cowen, 2004). Although Great Barrier Reef (GBR) shelf waters are generally well mixed (Luick et al., 2007), *L. carponotatus* larvae may perform vertical migrations. Accordingly, the self-seeding percentage we projected would probably have been higher if our behavioral model had included vertical migration. Further, our assumption that recruits to OTI could only come from reefs in the CBG would have also affected the projected self-seeding rate. In justifying this assumption, we argued that a majority of *L. carponotatus* recruits to OTI probably come from within the CBG based on: (1) the well documented reduction in dispersal kernels (the potential for successful dispersal connections) with distance from natal reefs (Jones, 2015; Williamson et al., 2016) and (2) the results of a genetic parentage analysis of two coral trout species, *Plectropomus maculatus* and *Plectropomus leopardus*, in the southern GBR (Williamson et al., 2016). Multidirectional larval dispersal was recorded in the genetic parentage analysis and some coral trout recruits originating from the Keppel Islands and the Percy Island Group, ∼100 and ∼250 km from the CBG respectively, successfully dispersed to reefs in the CBG. It is, therefore, possible that some *L. carponotatus* larvae make the same journey. An additional source of larvae to the CBG could be the Swain Reefs ∼150 km away. With the method applied in this study, considering sources of recruits from outside of the CBG would have reduced the self-seeding rate projected for OTI. As equal numbers of larvae were released from all seed locations, the proportion of the total pool of larvae originating from OTI would have been reduced. Ideally, the numbers of larvae released would have been scaled to reflect the different reproductive capacities of the local adult populations inhabiting the different reefs, but the data required to make this adjustment were not available. The sources of *L. carponotatus* recruits to OTI could be identified more definitively through genetic parentage analyses (e.g., Williamson et al., 2016) or mark, recapture experiments, where the otoliths of larvae are tagged with maternally transmitted stable isotopes (e.g., Almany et al., 2007).

The Recruitment of *Lutjanus carponotatus* to One Tree Island

There was considerable inter-annual variability in the abundance of *L. carponotatus* recruits recorded at OTI. In some years there was total recruitment failure, where no recruits were observed. While variability in recruitment is common in coral reef ecosystems, the virtual absence of recruits seems unusually extreme (Doherty, 2002; DeMartini et al., 2013), especially since lutjanid larvae are typically robust and strong swimming (Leis,

2006) and some self-recruitment would be expected (Jones, 2015). We found that the abundance of recruits varied with the prevalence of survivor specific favorable winds during the period of peak production, when the recruits were most likely to be in their larval stage. Biophysical modeling suggested that the identified winds drove currents that kept the larval plume concentrated in the CBG, reducing larval mortality through expatriation. The larval period is the only stage in the lifecycle of *L. carponotatus* where the wind-driven current could feasibly have a direct effect on mortality because *L. carponotatus* are strong swimming and are reef-associated after settlement. The significance of the correlation between recruitment and favorable winds suggests that variability in recruitment was influenced by physical forcing during the larval stage. Physical forcings that affect larval mortality have previously been linked to the recruitment of commercially important species, where recruitment into the fishery occurs years after the larvae are spawned (e.g., Caputi et al., 1996; Wilderbuer et al., 2013). However, robust empirical models where physical conditions are good predictors of recruitment are rare and scarcely used in fisheries management (Skern-Mauritzen et al., 2016). There are exceptions, such as the use of an upwelling index in the models predicting the recruitment of Anchovy, *Engraulis encrasicholus*, to the Bay of Biscay in the northeast Atlantic Ocean (Skern-Mauritzen et al., 2016). Here we have provided a model to predict when the recruitment of *L. carponotatus* to OTI will be good or bad; similar empirical models may have broader applicability in the CBG, and in other reef complexes in the GBR. As ocean monitoring technologies improve, enhancing our ability to forecast biological indices, scientists and end-users must communicate effectively to utilize such empirical models to their full potential (Payne et al., 2017).

The correlation we present here only considers the effects of larval mortality on recruit abundance, specifically by expatriation from wind driven currents. The significance of the relationship suggests that larval mortality by expatriation is an important determinant of the recruitment of *L. carponotatus* to OTI. However, there was considerable unexplained variability in the relationship which was probably attributable to other reproductive and pre and post settlement processes known to influence recruitment. Further, the implications of the assumptions made in the biophysical modeling were discussed previously; assumptions were similarly made in the empirical modeling which would have contributed to the unexplained variability in the correlation.

The influence of variability in reproduction was not accounted for in our correlation. Firstly, variability in the reproductive capacity of adults can affect the magnitude of recruitment. The larval supply can be a good predictor of recruitment (Milicich et al., 1992), and it can be affected by fluctuations in spawner biomass (Jennings et al., 2001). We presented data showing that consistently high numbers of *L. carponotatus* adults were present at OTI over the 23-year sampling period; however, there were no data available for the numbers of *L. carponotatus* adults at other reefs in the CBG or the surrounding region. The magnitude of fluctuations in the biomass of the stock of *L. carponotatus* contributing offspring to OTI is therefore unknown. Changes in fecundity can also affect the reproductive capacity of a population. The fecundity of an individual can depend on the availability of resources, where the abundance/scarcity of resources determines their allocation toward reproduction (Duponchelle et al., 2000). Upwelling can boost productivity in coral reefs which are generally located in oligotrophic surface waters (Wolanski and Delesalle, 1995). Increased productivity could have a trickle up affect whereby an increase in primary production boosts secondary production, increasing the abundance of the prey species targeted by the predatory *L. carponotatus* (Jennings et al., 2001). Multiple sources of upwelling have been identified in the southern GBR, including strong northerly winds and the Capricorn Eddy (CE; Weeks et al., 2010; Mao and Luick, 2014). Finally, when we correlated the prevalence of favorable winds with recruitment, we only considered winds, and therefore spawning, in the period of peak *L. carponotatus* production (October to January; Russell et al., 1977; Kritzer, 2004). Some *L. carponotatus* clearly spawn outside of these months. Kritzer (2004) found that at least 50% of the ovaries from *L. carponotatus* females in the Palm and Lizard Island groups were ripe for 7 months of the year from September to February and recruits from this study were spawned in May. Variability in the magnitude and timing of spawning can cause large fluctuations in the supply of larvae within and among spawning seasons (Milicich et al., 1992). Such fluctuations can be more pronounced at the southern extremes of the distributions of species (e.g., Fowler, 1991), and the CBG is at the southern end of the range of *L. carponotatus*. Given the expected irregularity in larval production, misalignments could have occurred where favorable winds were present when larval production was low and vice versa. Such misalignments would weaken the relationship between recruitment and the prevalence of favorable winds.

While retention under favorable winds was considered in the presented correlation, numerous other pre-settlement processes can affect the magnitude of recruitment. Larval mortality can affect larval supply and, subsequently, recruitment (Milicich et al., 1992). There are many sources of larval mortality including starvation (e.g., Cushing, 1975, 1990), predation (e.g., Moller, 1984; McGurk, 1986) and expatriation (e.g., Sponaugle and Pinkard, 2004). Starvation can be a major source of mortality in fish larvae (Leggett and Deblois, 1994). As with the adults, the upwelling of nutrient rich water can increase the availability of species that larvae prey on, and improve the nutritional content of prey items (Jennings et al., 2001). The larval mortality rate of *L. carponotatus* larvae in the southern GBR could be reduced if their spawning coincides with an upwelling event, as proposed in the match mismatch hypothesis (Cushing, 1990). In this study, we defined "favorable winds" as balanced; if the northerly winds linked to upwelling in the southern GBR formed part of a balanced wind cycle, they could have been included in the correlation through being categorized as "favourable." In this way, differential mortality from starvation could have indirectly influenced the presented correlation. Further, predation pressure on the eggs and larvae of marine species can be intense (Purcell, 1985; Bailey and Houde, 1989), and can vary with physical conditions (e.g., Frank and Leggett, 1982). It is possible that inter-annual variability in the rate of predation on *L.*

carponotatus eggs and larvae influenced recruitment to OTI but there are no data available to examine this possibility. Finally, while the impact of larval retention under favorable winds was examined in the presented correlation, the impact of retention/expatriation in other scenarios was not considered. Larvae can be retained in the CBG under non-favorable wind conditions, as demonstrated with the biophysical model. Settlers arriving under these alternate wind conditions would degrade the presented relationship between the prevalence of survivor specific winds and recruitment. Additionally, the correlation we presented does not incorporate data on the influences of other oceanographic forces, such as the CE and the North Caledonian Jet (NCJ). The CE can greatly affect the currents in the CBG (present study; Mao and Luick, 2014) and the NCJ is a principal driver of the currents in the GBR system (Andrews and Clegg, 1989; Wolanski, 1994). Inter-annual variability in the prevalence and strength of the CE, and the strength of the NCJ could therefore greatly influence larval mortality through expatriation, independent of the influence of favorable winds. Further, we did not examine the potential for these and other dispersive forces to bring recruits from reefs outside of the CBG to OTI. Post settlement mortality (Hixon, 2015) can also affect recruitment patterns. A 13–16 month gap between peak larval production and recruitment was incorporated into the model, meaning recruits could have been settled for up to 15 months before recruitment was measured. Given this lag, and the substantial mortality newly settled fish can experience (Sale and Ferrell, 1988), the decoupling of a settlement signal from the later measure of recruitment is plausible. Variation in habitat quality (Jones et al., 2004), predation (Hixon, 2015), and density dependant mortality (Schmitt and Holbrook, 1999) can all affect the survivorship of recruits.

The Wind and Recruitment

Wind patterns had a great influence on the modeled larval dispersal trajectories and, therefore, probably greatly affected the recruitment of *L. carponotatus* to OTI. The impact of the wind was unsurprising given the CBG lies on a shallow section of the Australian continental shelf, and winds can be the principal driver of currents in shallow waters (e.g., Pattrick et al., 2013). Indeed, Mao and Luick (2014) found strong correlations between the winds and the surface currents in the CBG region. In this study we found that fish that had successfully arrived at OTI survived either longshore SSE winds with a balanced cross shelf component, or cross shelf ENE winds with a balanced longshore component. Both conditions induced insubstantial, unidirectional movement in the larval plume, keeping it concentrated in the CBG. Consequently, the scenarios with these winds had the greatest recruitment potential. Other studies have similarly found that wind induced oscillatory flow patterns can concentrate plumes of fish larvae, facilitating recruitment (Basterretxea et al., 2013). Further, the winds identified to be favorable for recruitment in this study were highly seasonal. The seasonality of favorable recruitment conditions has been documented in multiple environments, from coral reefs in the Philippines (Abesamis and Russ, 2010; Abesamis et al., 2017) to coastal fisheries in the NW Mediterranean (Basterretxea et al., 2012).

The larval supply of lutjanids to OTI over the course of 1 month has previously been linked to periods (8/9 days) of offshore winds advecting larvae to the island from the NW (Kingsford and Finn, 1997). These winds could have been part of an alternating longshore wind cycle, like the cycle that occurred when the *L. carponotatus* from the 2015 cohort were in the plankton. The conclusions of Kingsford and Finn (1997) reinforce the importance of wind to recruitment in the CBG region, but suggest that there may be a greater variety of favorable wind scenarios than were identified in this study. Logically, the transportation of larvae to OTI from the NW would be favorable for recruitment if larval production was high at reefs NW of OTI. The direction of larval transport would change over an extended spawning season, such as that of *L. carponotatus*, due to the seasonality of the winds in the region. Further research into the spatial and temporal variability in *L. carponotatus* reproductive output, in relation to the seasonality of the wind, may refine our understanding of recruitment variability.

Relatedly, "balanced winds," as defined in this paper, could arise from numerous scenarios where there are alternations in the strength and duration of the longshore and cross shelf winds. Each distinct scenario would have a unique influence on larval transportation and survival. For example, the dispersive forces acting on a larval plume could be reduced during a wind relaxation (Abesamis and Russ, 2010; Cuif et al., 2014). Conversely, the waves generated by strong winds could increase mixing and induce a current shear (Simpson and Dickey, 1981). A more detailed knowledge of the composition of "balanced winds" could be gained through analyzing the variability in the wind. Time series analysis techniques, such as spectral analysis (e.g., Taggart and Leggett, 1987), could be used to decompose the variability in the wind. Alternatively, future research could look at the frequency of calm periods or extreme events, analogous to the approach of Peterman and Bradford (1987) who found that the frequency of low wind speed periods (Lasker events) during the northern anchovy (*Engraulis mordax*) spawning season was correlated with the larval mortality rate.

The Capricorn Eddy

The CE was detrimental for recruitment in most scenarios as it advected large numbers of larvae eastward from the CBG into oceanic waters. Sponaugle et al. (2005) found that the arrival of multi-taxa larval pulses to reefs in the Florida Keys coincided with the passage of sub mesoscale eddies with diameters of 10 to 40 km, produced from the decay of larger mesoscale eddies 100–200 km in diameter. The little researched CE appears to have a diameter of approximately 100 km when present (Weeks et al., 2010; Mao and Luick, 2014). The CE may retain the larvae that it advects from reefs in the CBG, and from the Swain Reefs to the north of the CBG. However, the timely transport of these larvae back to reefal waters within the 22 to 28 day PLD of *L. carponotatus* is unlikely given the size of the CE in relation to the sub-mesoscale eddies linked to favorable recruitment in the Florida Keys. As mentioned previously, the CE can be a source of upwelling in the southern GBR (Weeks et al., 2010; Mao and Luick, 2014). Consequently, larval mortality from starvation may be reduced when the CE is present, and the settlers that arrive at OTI may be in better condition than those that were in the plankton when the CE was absent. In this way, the positive ecological effects of the CE could counteract its negative dispersive effects. Research into the characteristics of the CE is required to better understand its ecological impact on the southern GBR.

The Importance of Larval Swimming Behavior

The inclusion of swimming behavior caused order of magnitude increases in the number of potential settlers present around OTI at the end of the PLD. Larval mortality from expatriation was reduced when swimming was included, as indicated by the modeled increase in the return rate. Wolanski and Kingsford (2014) also calculated the percentage of modeled passive and swimming larvae seeded from OTI that had returned to OTI by the end of a PLD. They sequentially varied the physical and biological parameterization of a biophysical model and similarly found that the inclusion of behavior improved larval survival. The projected rate of return ranged from 0.6 to 5.9% when the larvae were modeled as passive. When they were programmed to swim the upper limit of the modeled rate of return increased significantly, with the projected rates ranging from 0.4 to 28.8%. Many studies have similarly found that the inclusion of behavior in models vastly improved the predicted larval retention and subsequent recruitment (e.g., Paris et al., 2007; Butler et al., 2011; Basterretxea et al., 2013). In addition to improving the overall projected recruitment, when larvae were made to swim, they counteracted the adverse dispersive forces of strong winds and the CE. Consequently, the relative favorability of the modeled oceanographic conditions changed so equivalent or greater numbers of potential settlers were recorded in the scenarios with strong winds and/or the CE, compared to the scenario with average winds and no CE. Such fundamental changes in results have been recorded in other biophysical modeling studies following the inclusion of behavior. For example, Paris et al. (2007) found that the inclusion of diel vertical migration behavior and larval mortality into a biophysical model of the western Caribbean changed the simulated connectivity in the region. The present study supports the consensus that the inclusion of behavior in biophysical models is critical if the organism being modeled can influence its dispersion (Wolanski, 2017). This has been shown true for a range of species, from fishes and corals with short PLD's (e.g., Wolanski and Kingsford, 2014) to crustaceans with long PLD's (e.g., Butler et al., 2011) and jellyfishes with adult pelagic phases (e.g., Fossette et al., 2015; Schlaefer et al., 2018).

CONCLUSIONS

The recruitment of *L. carponotatus* to OTI was highly variable over the 23-year study period. The gains in adult abundance that followed sustained recruitment suggested that the size of the adult population was largely determined through variation in recruitment. The potential for *L. carponotatus* larvae from the CBG to recruit to OTI was greatest in the currents driven by the winds that were present during the pelagic phases of the fish we collected at OTI. There was a significant positive relationship between the prevalence of these wind conditions during the period of peak *L. carponotatus* larval production and the measured recruitment in the following year. The prevalence of the identified winds could therefore be used as a proxy to predict recruitment. Larvae arrived at OTI in comparably smaller numbers in the modeling scenarios forced with either average or strong winds, and with or without the CE. This study highlighted the substantial impact that the inclusion of larval swimming behavior can have on the predicted recruitment, in accordance with other biophysical modeling studies. We worked at a fine temporal resolution, identifying and modeling the specific pelagic conditions survived by fish that had successfully arrived at OTI. The favorable winds may not have been identified if the investigation was conducted at a coarser temporal resolution, demonstrating the efficacy of studying the conditions experienced by survivors.

ETHICS STATEMENT

This study was carried out in accordance with the recommendations of James Cook Universities policies, procedures and guidelines, Animal Ethics Committee at James Cook University. The protocol was approved by the Animal Ethics Committee at James Cook University.

AUTHOR CONTRIBUTIONS

JS, EW, and MK: Study conception and design; JS, EW, and MK: Data collection and analysis; JS, EW, and JL: Biophysical modeling; JS: Drafting the manuscript; JS, EW, JL, and MK: Revising the manuscript.

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frontiers in Marine Science

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Mechanisms of Cross-Shore Transport and Spatial Variability of Phytoplankton on a Rip-Channeled Beach

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We investigated whether cross-shore distributions of coastal phytoplankton to the surf zone are controlled by hydrodynamics and their biological characteristics. Data from a rip-channeled beach indicate that concentrations of phytoplankton are higher in the surf zone than offshore. To examine how phytoplankton is transported toward the shore, we used a coupled biophysical model, comprised of a 3D physical model of coastal dynamics and an individual-based model (IBM) for tracking phytoplankton on the rip-channeled beach. Waves and wind in the biophysical model were parameterized by the conditions during the sampling period. Previous studies indicated that growth rates of phytoplankton can be enhanced by high turbulence, which might contribute to high phytoplankton concentration in the surf zone. Some numerical and laboratory works showed that turbulence can also increase the downward velocity of phytoplankton, which could be carried by onshore bottom currents and remain in the surf zone. Furthermore, we adapted the IBM with the theoretical model of diurnal vertical migration (DVM) for phytoplankton. The theoretical DVM works as follows: in the morning, phytoplankton cells adhere to air bubbles and stay at the surface and close to the shore in the daytime because onshore wind and surface current direction is usually onshore; in the late afternoon, the cells switch their attachment from air bubbles to sand grains and sink to the bottom where the water flow is normally onshore at night. Finally, depth-varying growth of phytoplankton was also incorporated into the DVM module. Simulations using neutral passive particles do not give the expected results of observed patterns. All tested mechanisms, i.e., wind- and wave-driven currents, rip-current circulation, turbulence-driven growth and sinking, DVM, and depth-varying growth, enhanced onshore phytoplankton migration and cell concentrations in the surf zone, indicating that both biological traits and physical factors can be essential to phytoplankton cross-shore transport and spatial variability. Our model is open to be modified and re-parameterized, followed by further analysis and validation, so that it can be more adequate for ecological assessment of coastal areas.

Keywords: phytoplankton, cross-shore transport, surf zone, rip current, turbulence, vertical migration, cell growth

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INTRODUCTION

Phytoplankton dynamics in coastal water largely influence marine ecosystems, fisheries, and coastal communities. For example, with favorable environmental conditions, phytoplankton can overgrow and cause harmful algal blooms (HABs) that often increase levels of toxic substances in the coastal area and the toxins accumulate in intertidal animals, and humans can suffer poisoning by consuming those toxic animals (Landsberg, 2002). Since many HAB species reside offshore, it is important to understand how they are transported to shore and possibly enter the surf zone, which is considered a "semi-permeable barrier" (Rilov et al., 2008; Shanks et al., 2010). As Shanks et al. (2016) showed, surf zone hydrodynamics affect onshore transport of *Pseudo-nitzschia*, one of the species causing HABs. Recent studies revealed that onshore larval migration can be influenced by surf zone hydrodynamics and characteristics of larvae (Fujimura et al., 2014, 2017; Shanks et al., 2015, 2017, 2018; Morgan et al., 2016, 2017); however, mechanisms of onshore transport of phytoplankton are not well understood.

Phytoplankton cannot be modeled as simple passive particles; some phytoplankton species can float, sink, or swim (Smayda, 1970, 2010). In turbulent conditions, larvae of various intertidal invertebrate species sink to the bottom (Denny and Shibata, 1989; Butman, 1990; Fuchs et al., 2004; Roy et al., 2012) or actively move downwards (Fuchs et al., 2013) that can be essential traits for onshore larval migration as a model study showed (Fujimura et al., 2014). Likewise, sinking velocity of phytoplankton cells may be increased by turbulence possibly with a different mechanism (Ruiz et al., 2004; Macías et al., 2013). This might be due to preferential downward movement of particles along the peripheries of local vortical structures (Wang and Maxey, 1993). With the same vortical mechanism, the floating velocity of positively buoyant phytoplankton cells may be enhanced by turbulence. Additionally, some phytoplankton species swim with flagella or cilia. These floating and swimming behaviors were not considered in our study.

Spatial distributions of phytoplankton in the coastal area may not be controlled only by transport, but also cell growth. Variability in growth rates of phytoplankton under different environments can make their distribution patterns more complicated. For instance, Savidge (1981) showed high turbulence could increase phytoplankton growth rate about 25–75%. This may have resulted from higher levels of exposure to light and/or nutrient uptake in turbulence.

There is also diurnal periodicity in phytoplankton. Talbot et al. (1990) proposed the following diurnal vertical migration (DVM) model of surf zone phytoplankton species based on the series of their observational studies. At night, phytoplankton cells stay on the bottom by attaching to sediment with mucus they produce. In the morning, they lose the mucus and enter the water column by turbulent flows in the surf zone. Within the water column of the surf zone, they adhere to air bubbles produced by breaking waves, and increase their buoyancy. The cells float on the surface and grow in the daytime. During late afternoon, the cells start developing the mucus again and attach to sand grains to sink to the bottom. Mechanisms of formation and shedding of mucus as well as cells attaching to and detaching from air bubbles or sand grains have not been well studied. An ability to float at the surface by attaching to air bubbles or forming a semi-stable foam consisting of many small bubbles can be found in surf zone diatom species (Lewin and Schaefer, 1983). We combined the DVM model with a typical diurnal land-sea breeze cycle (i.e., onshore wind during the day and offshore wind at night). We hypothesized that phytoplankton cells stay near the surface and are kept in the surf zone by the sea breeze-driven currents during the daytime, and stay on the bottom where they are pushed toward shore by wave-driven bottom currents in the nighttime (**Figure 1**). Wave stress in the bottom boundary layer induces so-called benthic streaming, a bottom current flowing in the direction of wave propagation (Longuet-Higgins, 1953). Plankton near the bottom may be transported shoreward by streaming (Fujimura et al., 2014). Streaming may be weakened during daytime onshore wind events in order to balance with onshore surface flow (**Figure 1**).

Beach morphology also affects cross-shore transport of plankton (Shanks et al., 2010, 2017, 2018; Fujimura et al., 2013; Morgan et al., 2017). Beaches can be classified as a dissipative beach with a wide surf zone and flat slope, intermediate, or reflective beach with a narrow surf zone and steep slope (Wright and Short, 1984; McLachlan and Brown, 2006). Surf zone phytoplankton taxa are found only at dissipative and intermediate beaches, but not in more reflective surf zones (Lewin and Schaefer, 1983; Talbot et al., 1990; Shanks et al., 2018). In this study, we focused on an intermediate beach where cross-shore exchange is enhanced by rip currents. There are several types of rip currents (Dalrymple et al., 2011; Castelle et al., 2016), but here we considered bathymetrically-controlled rip currents (**Figure 2**). When waves approach perpendicular to shore, onshore currents converge toward shoals due to wave refraction, then alongshore feeder currents accumulated in rip channels, causing offshore-directed rip currents. Rip currents weaken offshore and merge with onshore currents. This pattern often forms rip circulations that entrain and concentrate phytoplankton cells (Talbot and Bate, 1987).

A field study at a rip-channeled beach showed that concentrations of coastal phytoplankton taxa are much higher in the rip channels than offshore or over the shoals (Shanks et al., 2018). It is very likely that surf zone hydrodynamics influence such spatial variability; however, characteristics of phytoplankton should also affect the concentration of phytoplankton within the surf zone, since completely passive particles cannot transport toward shore easily (Fujimura et al., 2014).

This study was to uncover the role of physical forcing and ecological traits in coastal phytoplankton dynamics at a relatively small scale. Here, we added theoretical parameters to our model of cross-shore phytoplankton transport. We tested the effects of turbulence-driven sinking and growth within the surf zone on onshore phytoplankton transport and the concentration of phytoplankton within the surf zone. Our model built upon that proposed by Talbot et al. (1990) with the addition of diurnal wind cycle at a rip-channeled beach. Modeled phytoplankton were released at two locations: offshore to examine how typical coastal phytoplankton taxa are transported onshore and increase

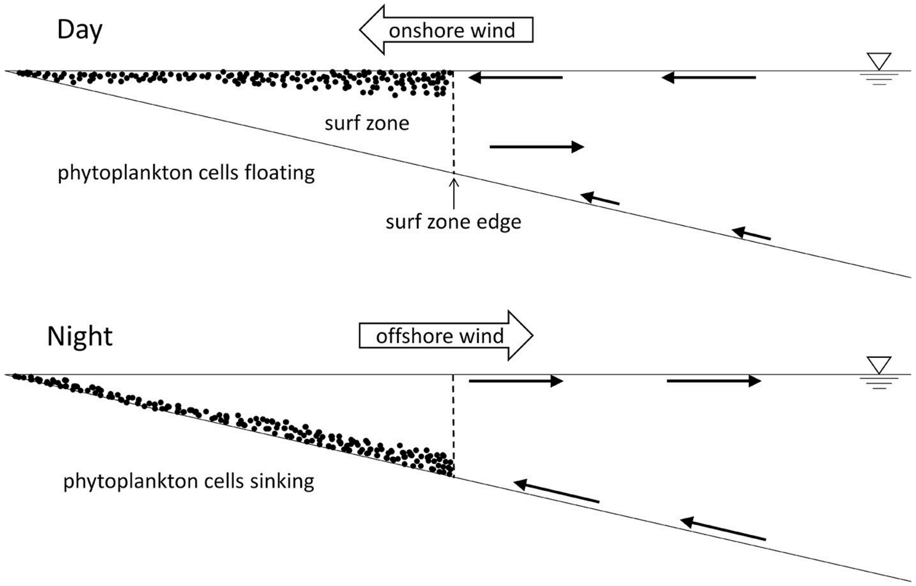

FIGURE 1 | Theoretical model of the diurnal vertical migration of phytoplankton in the surf zone with a diurnal wind cycle. Dots represent phytoplankton cells. Arrows show flow directions. Relatively short arrows on the bottom during the day indicate streaming weakened by wind-driven onshore surface currents.

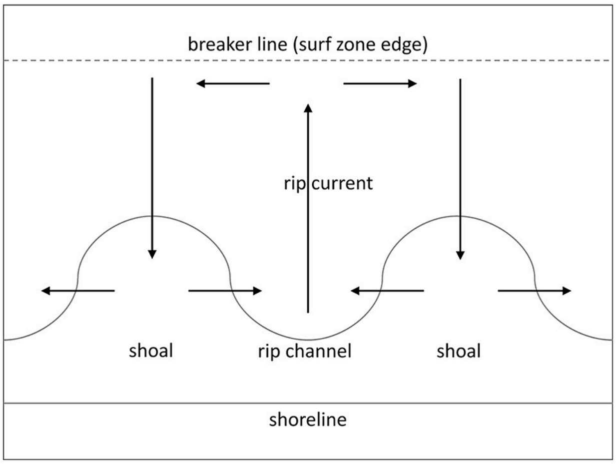

FIGURE 2 | Schematic diagram of water currents (arrows) at a rip-channeled beach. Waves approach shore normal. Curve indicates an isobath.

cell concentrations, and how surf zone taxa return to the surf zone; and inside the surf zone to examine how the coastal and surf zone phytoplankton taxa are retained in the surf zone and increase concentrations.

METHODS

Study Site

Bathymetry and wave data were collected at Sand City beach (36° 36′57″ N, 121° 51′15″ W), Monterey Bay, California in the summer of 2010. This area receives a strong sea breeze during the daytime and little, if any, land breeze at night (Hendrickson and MacMahan, 2009), and we observed the same wind pattern during the fieldwork. Bathymetry was taken with a personal watercraft equipped with sonar and a Global Positioning System (GPS), and a person walking with a GPS for shallow bottom. This location is characterized as an intermediate beach (Wright and Short, 1984) and rip channels and shoals are developed (**Figure 3**). Wave data were collected by acoustic Doppler current profilers deployed at 11 m water depth. The average wave direction during the field experiment was perpendicular to the shoreline (**Figure 3**). Numerous studies described hydrodynamics of this beach (MacMahan et al., 2004, 2010; Reniers et al., 2009, 2010; Fujimura et al., 2013, 2014; Brown et al., 2015). Typically, bathymetric rip currents and corresponding eddies are formed here as described in **Figure 2**.

Hydrodynamic Model

Three-dimensional hydrodynamic model simulations have been performed with Delft 3D which comprises FLOW (Deltares, 2011a) and WAVE (Deltares, 2011b) modules. All hydrodynamic simulations followed Fujimura et al. (2014) except for modeling durations and wind and wave conditions. For all model cases, we used only regular normally incident waves based on the averaged measurement data, and included Stokes drift (Stokes, 1847), a wave-related time-averaged volumetric transport in the direction of wave propagation. Fujimura et al. (2014) showed that Stokes drift is an essential part of onshore particle transport.

We considered situations without wind and with a diurnal wind cycle. In the no-wind condition, the model was run only with wave-driven currents for 48 h. For the diurnal wind cycle, a simulation started with constant offshore wind (2 m s^{-1}) for the first 12 h, linearly changed to onshore wind (6.0 m s^{-1}) in

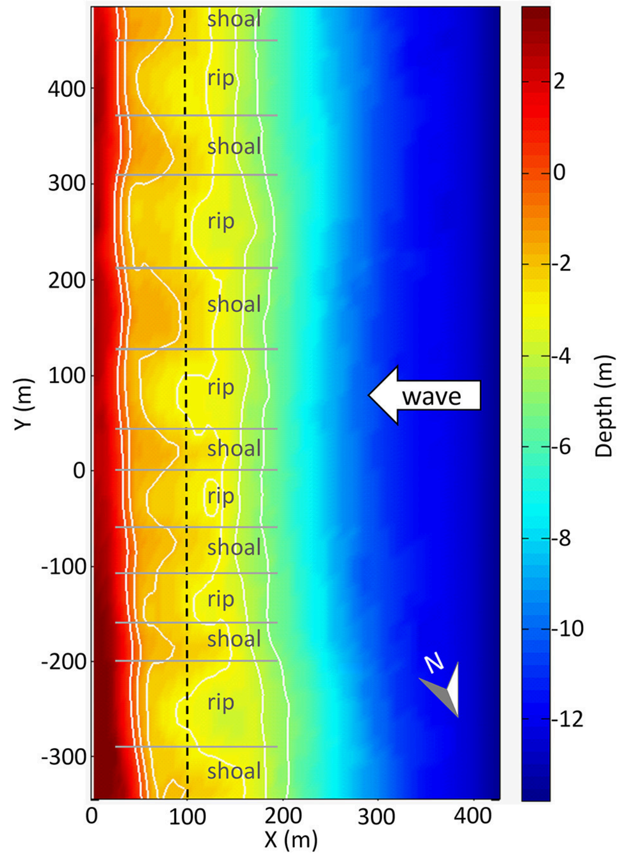

FIGURE 3 | Bathymetry at Sand City beach. White isobaths are in 1 m increments from depth of 0 m (shoreline) to 5 m. Black dashed line at 100 m approximates the surf zone edge (breaker line). The modeled wave angle obtained from time-averaged field data are indicated by the large arrow. Ranges of rip channels and shoals are indicated.

1 h and lasting for 24 h, then gradually returned to an offshore wind in 1 h. The wind again gradually shifted from offshore to onshore wind at 36 h, and the model was running with the constant onshore wind until 48 h. The first and third quarters of the simulation (0–12 h and 24–36 h) were considered as daytime, while the second and fourth quarters (12–24 h and 36–48 h) were simulated as nighttime.

Phytoplankton Transport Model

Modeled physical parameters (i.e., water currents, waves, eddy diffusivities and turbulence) and bathymetry were transferred to an individual-based model (IBM). We adapted the IBM code developed by Fujimura et al. (2014). We kept basic functions, such as the 4th order Runge-Kutta method for advection, random walk based on simulated diffusivities, and the boundary conditions from the open-source connectivity modeling system (Paris et al., 2013).

A basic vertical velocity of each phytoplankton cell was downward $w_p = -1.2 \times 10^{-5}$ m s^{-1} (1 m d^{-1}), which is a typical sinking rate of phytoplankton (Smayda, 1970). As we mentioned earlier, sinking velocity of cells may be increased by turbulence; thus, we assumed that cells sink at $w_{sink} = -2.5 \times 10^{-3}$ m s^{-1} when the turbulence energy dissipation rate is $\varepsilon > 10^{-5}$ m^2 s^{-3} (Ruiz et al., 2004). Turbulence greater than this threshold can be seen in the surf zone and some part of bottom boundary layer.

The total velocity components u_{tot} (cross-shore), v_{tot} (alongshore), and w_{tot} (vertical) are:

$$u_{tot} = u_{adv} + u_{diff} \tag{1}$$

$$v_{tot} = v_{adv} + v_{diff} \tag{2}$$

$$w_{tot} = \begin{cases} w_{adv} + w_{diff} + w_p & \begin{cases} \text{if turbulence-driven sinking is not considered} \\ \varepsilon \le 10^{-5} \text{m}^2\text{s}^{-3} \end{cases} \\ w_{adv} + w_{diff} + w_{sink} & \varepsilon > 10^{-5} \text{m}^2\text{s}^{-3} \end{cases} \tag{3}$$

where u_{adv}, v_{adv}, and w_{adv} are advection flow velocities, and u_{diff}, v_{diff}, and w_{diff} are random velocities of all three spatial components (cross-shore, alongshore, and vertical direction, respectively). u_{adv} and v_{adv} are Lagrangian velocities (u_L, v_L), consist of Eulerian velocities (u_E, v_E) and Stokes drift.

We also added a growth rate that increases under high turbulence condition (Savidge, 1981). The main purpose of the model is to examine the difference between phytoplankton concentrations in the surf zone and offshore, so the total number of cells in the system does not matter. Hence, in this model, not all phytoplankton cells grow, but only cells in high turbulence can grow. Every hour, randomly selected particles where $\varepsilon > 10^{-5}$ m^2 s^{-3} are doubled in cell number. This ε is the same value as the threshold for the turbulence-driven sinking. The number of randomly selected cells per hour is:

$$N = N_t \frac{\mu r}{24} \tag{4}$$

where N_t is total cells in turbulence, μ is a specific growth rate of phytoplankton and r is a fraction of increased growth rate due to turbulence. Here we use $\mu = 0.5$ d^{-1} (Parsons et al., 1984) and $r = 0.5$ (Savidge, 1981).

Separately, the DVM model proposed by Talbot et al. (1990) was applied to our model case with a diurnal wind cycle. In our model, DVM was considered only within the surf zone ($X \le 100$ m, see **Figure 3**). As suggested by Talbot et al. (1990), phytoplankton cells float on the surface during the day, and sink to the bottom at night. Floating cells are attached to air bubbles in the surf zone (Talbot and Bate, 1988b; Shanks et al., 2018). We assumed that the diameter of air bubbles was 100 μm, a typical size in the surf zone (Deane, 1997; Deane and Stokes, 1999, 2002). Based on empirical data (Detsch, 1991), we estimated an upward velocity of the bubbles as $w_{air} = 6.0 \times 10^{-3}$ m s^{-1}. Sinking cells are assumed to be attached to sand grains in the water column (Talbot and Bate, 1988b). We chose a uniform grain size 0.3 mm in diameter, which is a typical size at Sand City beach (Gallagher et al., 2011) and can be suspended in the surf zone (Reniers et al., 2013). A sinking velocity of the grain $w_{sand} = -1.45 \times 10^{-2}$ m s^{-1} was calculated with Zhiyao et al. (2008). Therefore, for the DVM model, Equation 3 becomes:

$$w_{tot} = \begin{cases} w_{adv} + w_{diff} + w_p + w_{air} & \text{during the day} \\ w_{adv} + w_{diff} + w_p + w_{sand} & \text{during the night} \end{cases} \tag{5}$$

In addition, we considered here phytoplankton growth during the day with vertical variation in the surf zone. For the DVM model, we assumed that cell division can be observed in almost all phytoplankton on the surface, half of the phytoplankton in the water column, and a very small portion of phytoplankton on the bottom (Talbot et al., 1990). When the DVM model included the phytoplankton growth in the surf zone, we applied a growth rate of 1.0 d^{-1} to cells at the depth of ≤ 0.25 m, 0.5 d^{-1} to cells in the water column, and 0 d^{-1} to cells at ≥ 0.25 m above the sea bed.

We tested the effects of increased sinking velocity and growth rate of phytoplankton owing to turbulence with no-wind or diurnal wind condition, as well as the effect of DVM in the diurnal wind regime, on cross-shore phytoplankton transport. Each simulation run was 48 h. A total of 602 cells (86 alongshore × 7 vertical array) were released every hour from offshore ($X = 410$ m) to examine onshore transport of offshore phytoplankton taxa and a return rate of surf zone diatoms; or inside the surf zone ($X = 60$ m) to see an exit rate of offshore species and a retention rate of surf zone taxa. Only the last quarter of each simulation (36–48 h) was used for analysis. The earlier period (0–36 h) was used as a spin-up stage for initialization. The model cases and parameters are summarized in **Table 1**.

RESULTS

Cross-Shore Velocity Profiles

Alongshore- and time-averaged cross-shore velocity profiles are shown for the defined rip channels and shoals (**Figure 3**) within the surf zone ($X < 100$ m), and offshore ($X > 200$ m) in the total alongshore range (**Figure 4**). The result verified the theory that Stokes drift adds onshore forcing to Eulerian current. Shoal and rip current were apparent at $X = 75$ m, and bottom boundary streaming enhanced onshore bottom ($X \geq 200$ m).

Onshore wind induced onshore surface currents in the daytime (**Figure 4**). At night, offshore wind altered the flow condition similar to that in the no-wind regime. Flow directions in the surf zone did not change with wind directions although magnitudes slightly changed. As expected, bottom streaming was suppressed during the onshore wind event because of the mass balance needed at the bottom to counter the onshore surface flow. Overall, the cross-shore current fields produced were consistent with the concept presented in **Figure 1**.

Transport and Distribution of Phytoplankton

Many offshore-released phytoplankton cells were ejected from the domain (**Figure 5**). Phytoplankton were not effectively carried in the surf zone without turbulence-driven sinking. Turbulence-driven growth had little effect as growth was only enhanced when cells were within the surf zone.

In the diurnal wind regime, the number of offshore phytoplankton that were transported toward shore was highest in the case that the cells had the turbulence-driven growth and sinking, followed by the case with DVM and depth-varying growth (**Figure 5**). DVM somewhat enhanced onshore transport, but it was more effective at increasing the concentration of phytoplankton within the surf zone when the growth function was added. Interestingly, some phytoplankton cells without

TABLE 1 | Summary of modeled cases.

Simulation number	Release location	Diurnal wind cycle	Turbulence-driven growth	Turbulence-driven sinking	DVM	Depth-varying growth	Figure
1	Offshore						5A
2	Offshore		✓				5B
3	Offshore			✓			5C
4	Offshore		✓	✓			5D
5	Offshore	✓					5E
6	Offshore	✓	✓	✓			5F
7	Offshore	✓			✓		5G
8	Offshore	✓			✓	✓	5H
9	Surf zone						6A
10	Surf zone		✓				6B
11	Surf zone			✓			6C
12	Surf zone		✓	✓			6D
13	Surf zone	✓					6E
14	Surf zone	✓	✓	✓			6F
15	Surf zone	✓			✓		6G
16	Surf zone	✓			✓	✓	6H

Phytoplankton cells were released either at $X = 410$ m (offshore) or 60 m (within the surf zone). The wind condition was either no-wind or a diurnal wind cycle (daytime onshore breeze and nighttime offshore breeze). Diurnal vertical migration (DVM) was not included with turbulence-driven growth or sinking. Corresponding figures are indicated.

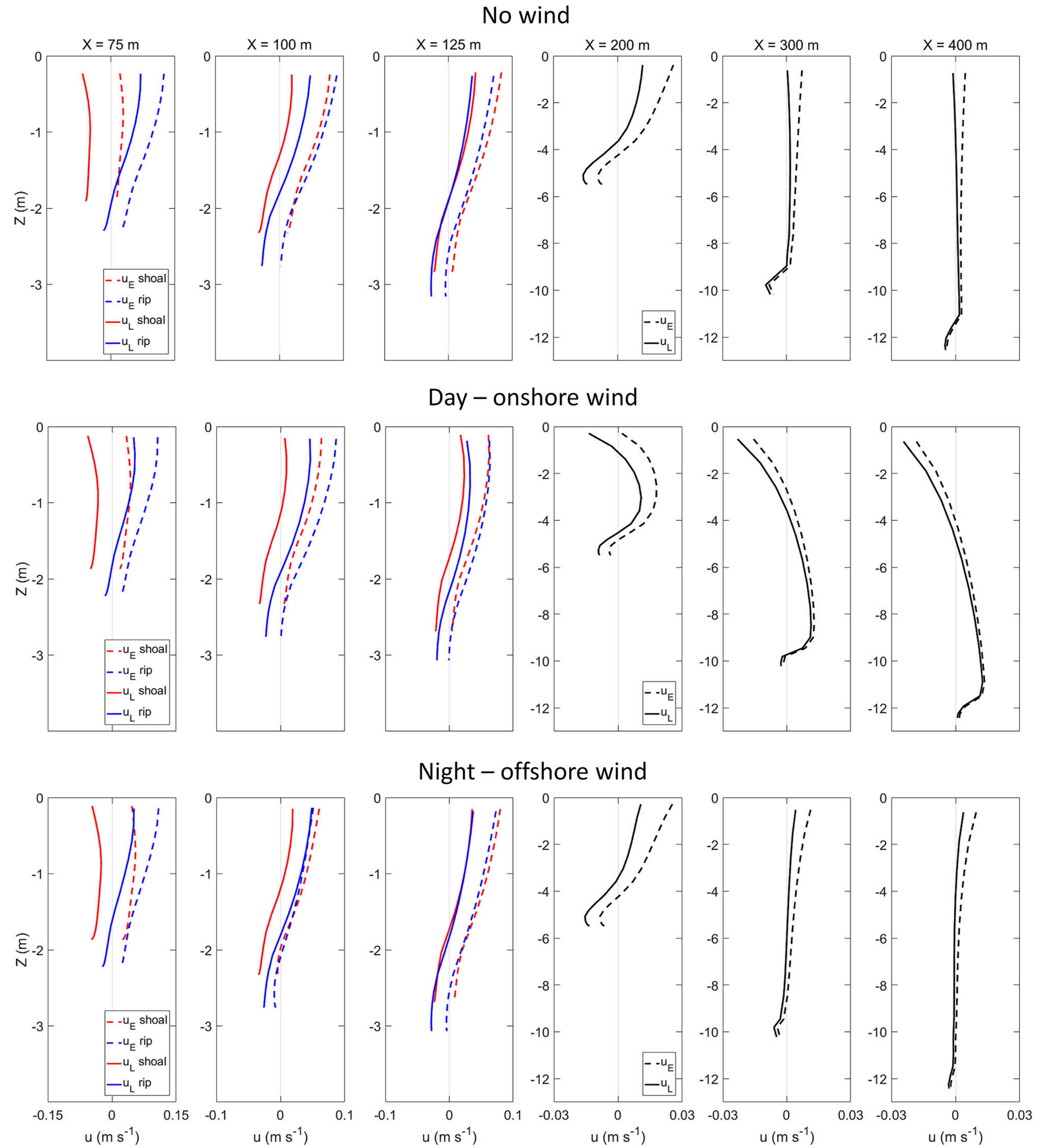

FIGURE 4 | Vertical profiles of alongshore- and time-averaged cross-shore velocities of the hydrodynamic model cases (upper panels) without wind and (middle panels) velocities averaged during the day (24–36 h), and (lower panels) night (36–48 h) in the diurnal wind cycle. Dashed line is Eulerian velocity (u_E) and solid line is Lagrangian velocity (u_L). The first three panels to the left are average velocities in the rip channels (blue) and on the shoals (red), and the others are averages over the total alongshore ranges (black). Positive and negative *u* values correspond to offshore and onshore currents, respectively. 75 m is within the surf zone and 100 m is at the breaker line.

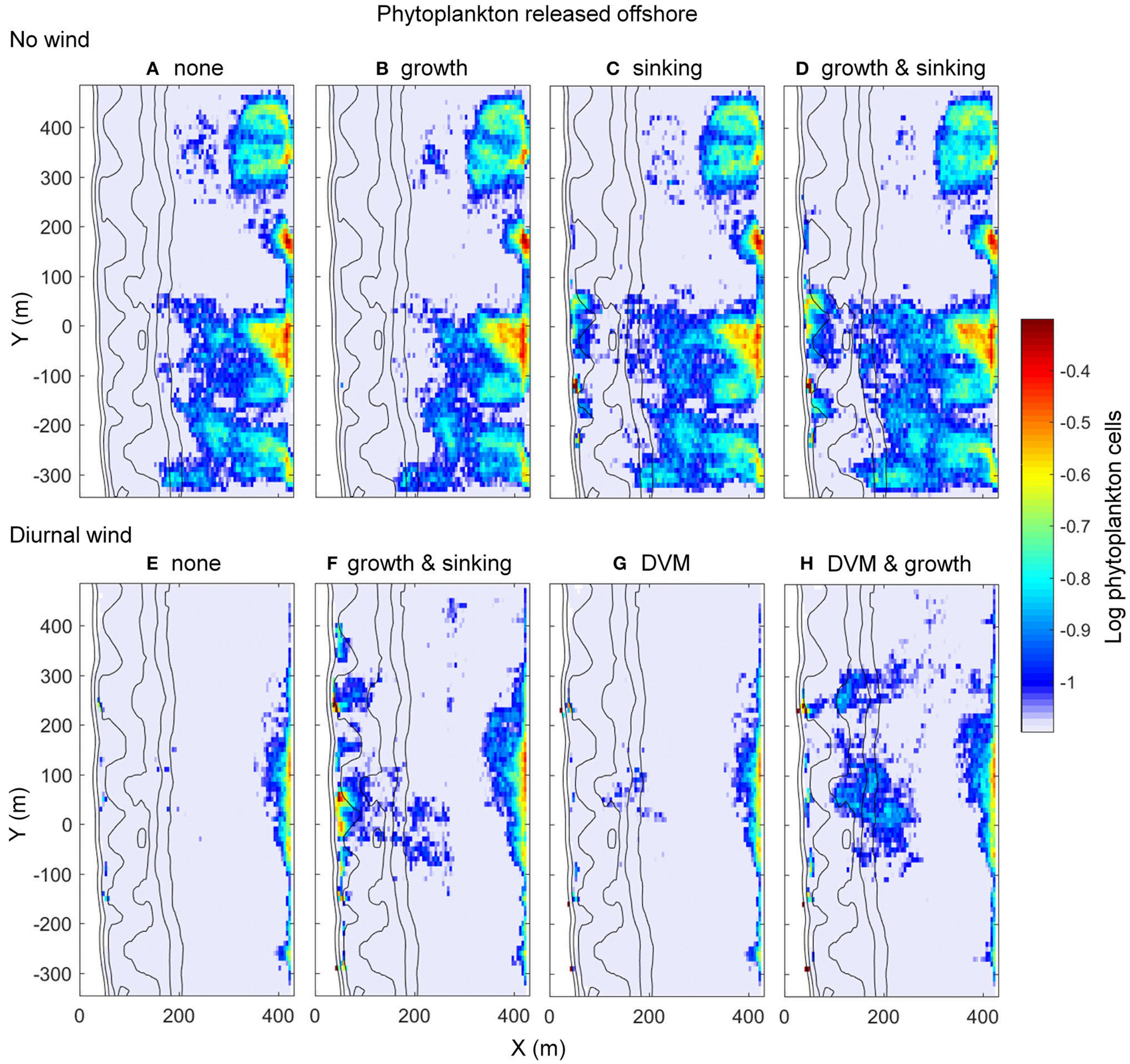

FIGURE 5 | Depth- and time-averaged number of cells per grid cell. Phytoplankton cells released offshore in **(A–D)** no-wind and **(E–H)** diurnal wind regime. Phytoplankton cells with **(A,E)** no growth, sinking, or DVM, **(B)** turbulence-driven growth, **(C)** turbulence-driven sinking, **(D,F)** both turbulence-driven growth and sinking, **(G)** DVM, and **(H)** DVM and depth-varying growth. Isobaths from 0 m (shoreline) to 5 m with 1 m increments are given.

turbulence-driven sinking and DVM were also carried to shore (**Figure 5E**).

When phytoplankton were released in the surf zone, all cases showed cell concentrations higher in the surf zone than offshore (**Figure 6**). Sinking with sand grains enhanced retention of cells in the surf zone. Surf zone concentration of phytoplankton released within the surf zone was highest in the case of the cells with DVM and depth-varying growth (**Figure 6H**); however, cell retention rate in the surf zone in this case was not high compared to the other cases as substantial quantities of phytoplankton seemed to be carried offshore (**Figure 6**). Phytoplankton with turbulence-driven growth and sinking tended to be retained and subsequently increased in the surf zone (**Figure 6F**). Similar to the offshore-released case, cells without any traits also tended to stay in the surf zone (**Figure 6E**).

Cell concentrations in the surf zone would become much higher than offshore over time because onshore cell flux (**Figure 5**) was higher than offshore cell flux (**Figure 6**). All (except for **Figures 5A,B**) cases showed the common distribution trend of phytoplankton (per unit area), that is, highest cell concentrations were found in the rip channels, followed by

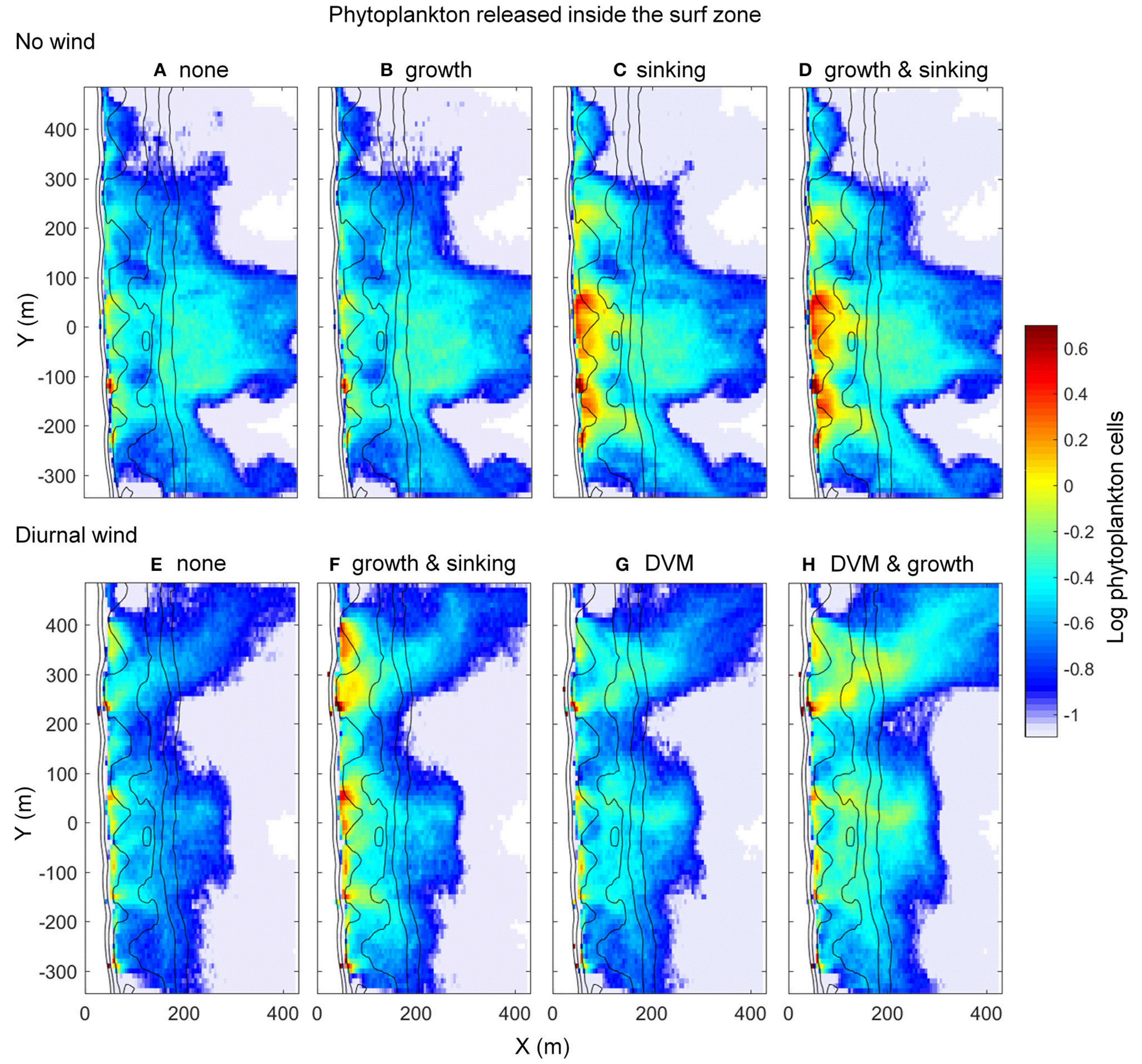

FIGURE 6 | Depth- and time-averaged number of cells per grid cell. Note that the color bar range is different form **Figure 5**. Phytoplankton cells released inside the surf zone in **(A–D)** no-wind and **(E–H)** diurnal wind regime. Phytoplankton cells with **(A,E)** no growth, sinking, or DVM, **(B)** turbulence-driven growth, **(C)** turbulence-driven sinking, **(D,F)** both turbulence-driven growth and sinking, **(G)** DVM, and **(H)** DVM and depth-varying growth. Isobaths from 0 m (shoreline) to 5 m with 1 m increments are given.

that over the shoals, and the smallest concentrations offshore (**Figures 5**, **6**).

Comparison Between No-Wind and Diurnal Wind Case

Phytoplankton without sinking, growth, and DVM were dispersed vertically in the no-wind condition (**Figure 7A**), whereas those in the diurnal wind condition tended to be concentrated near the bottom and surface (**Figures 7C,E**). Phytoplankton concentration at the surface extended offshore in the no-wind case (**Figure 7A**). A similar extension was formed at night in the diurnal wind case (**Figure 7C**), but not pronounced like in the no-wind case. Vertical velocities at X > 150 m during the day in the diurnal wind cycle directed downward (**Figure 7F**). Offshore vertical velocities (X > 200 m) at night tended to be slightly upward (**Figure 7D**), and neutral with a little variability in the no-wind regime (**Figure 7B**).

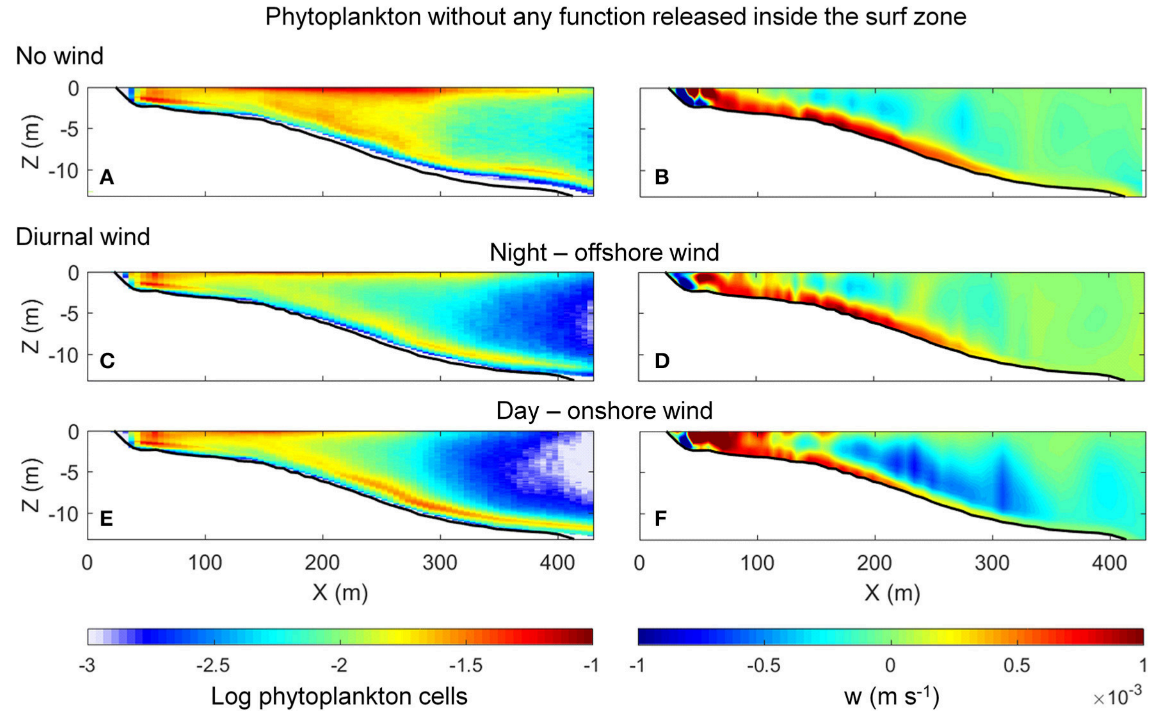

FIGURE 7 | (A,C,E) Alongshore- and time-averaged phytoplankton cells without growth, sinking, or DVM released inside the surf zone. **(B,D,F)** Alongshore- and time-averaged vertical velocities. **(A,B)** No-wind case. **(C,D)** Nighttime and **(E,F)** daytime of the diurnal wind cycle.

DISCUSSION

This modeling study suggests that turbulence-driven sinking may be an important mechanism for transport of phytoplankton into the surf zone, just like the sinking behavior of competent larvae in turbulence (Fujimura et al., 2014). Once phytoplankton enter the surf zone, their growth may be enhanced by turbulence, resulting in high cell concentration in the surf zone.

Our model showed that the diurnal wind cycle increased onshore transport (**Figures 5A,D** compared to **Figures 5E,F**) and reduced flushing rates of phytoplankton cells (**Figures 6A,D** compared to **Figures 6E,F**). These results were probably due to onshore wind, the major difference between no-wind and diurnal wind regimes. The modeled phytoplankton cells had a relatively small fall velocity ($w_p = -1.2 \times 10^{-5}$ m s^{-1}), which is 1–2 orders of magnitude smaller than the modeled vertical water velocities (**Figure 7**); thus, the vertical displacement of cells was affected by surrounding currents. In all cases, phytoplankton cells were brought to the surface by the upward flow in and near the surf zone (**Figure 7**). When wind was not applied, many of the cells were kept near the surface throughout the domain, and some cells were sinking or floating in the water column offshore (**Figure 7A**). In the diurnal wind cycle, cells floating near the surface were also carried offshore at night (**Figure 7C**), but upward currents kept them off from the water column (**Figures 7C,D**); furthermore, these cells were pushed back to the shore when the condition switched to onshore wind condition (**Figure 7E**). During the day, downward currents in the water column enhanced downward velocities of phytoplankton (**Figure 7F**), and transported via the onshore bottom currents although these were weakened due to balancing with onshore surface currents (**Figure 4**). Therefore, wind-driven onshore currents were likely to enhance phytoplankton transport toward the shore, while the constant wave-driven flow regime without wind caused higher phytoplankton flushing rates. The results were consistent with a study by Hendrickson and MacMahan (2009) who indicated that diurnal sea breeze is important for cross-shore transport.

Other physical forcing can play a role as well. Stokes drift represented by difference between u_L and u_E (**Figure 4**) added onshore forcing. Without Stokes drift, onshore transport of materials at the surface may be slower as shown by Fujimura et al. (2014). Bottom onshore currents and benthic streaming owing to wave forcing are also important especially when plankton are in the wave boundary layer. Alongshore variability (rip channels and shoals) can be another factor that increases onshore phytoplankton transport. Bathymetrically-controlled rip currents enhance shoaling to balance cross-shore currents. This bathymetric feature often forms a rip circulation with an eddy at its center where plankton may be trapped (Talbot and Bate, 1987; Fujimura et al., 2014; Shanks et al., 2017). Furthermore, flatter beach slopes (i.e., more dissipative beach) should be more conducive to onshore transport of plankton (Shanks et al., 2010, 2017, 2018; Fujimura et al., 2013; Morgan et al., 2016, 2017).

Our data showed that the concentrations of phytoplankton were highest in the rip channels, followed by that over the shoals, and lowest offshore. This pattern is the same as the larval distribution at the same beach (Fujimura et al., 2014; Morgan et al., 2016, 2017). High concentrations of plankton in the rip channels are possibly a result of the convergence of feeder currents (**Figure 2**). Our results partially agreed with Shanks et al. (2018) that phytoplankton concentrations in the surf zone were much higher than offshore. However, contrary to our study, their data showed that cell concentrations over the shoals were lower than offshore. This discrepancy might be due to the sampling scheme. They collected samples at 1 m depth in the surf zone and throughout the water column offshore, while we averaged phytoplankton cells in the water column everywhere. Hence, we recalculated the time-averaged number of cells over the shoals at 1 m ± 0.5 m. Nonetheless, modeled phytoplankton concentrations were still higher over the shoals than offshore in all cases although shoal to offshore ratios became smaller (e.g., for DVM with depth-varying growth case, 12:1 with original calculation, 2:1 with recalculation). More plausible reason for the discrepancy between Shanks et al. (2018) and our result was a lack of significant environmental parameters and/or phytoplankton traits and further investigation will be necessary for the model to reproduce such a distribution pattern of phytoplankton.

Limitations and Generality

Phytoplankton cells are suspended occasionally (e.g., in the ocean surface mixed layer) which has been supported by some studies showing that downward velocities of phytoplankton slowed in turbulent waters (e.g., Ruiz et al., 1996; Deleersnijder et al., 2006); nevertheless, this phenomenon can be seen only when turbulence level varies vertically (Ross, 2006; Macías et al., 2013). As the surf zone in our model was a more or less homogeneous layer with the turbulence energy dissipation rate $\varepsilon > 10^{-5}$ m^2 s^{-3}, the value used as the threshold obtained from the empirical data (Ruiz et al., 2004), the reduction of vertical velocity was ignored here. Vertical motion in turbulence is species-specific (Ruiz et al., 2004), while most studies on vertical velocities in turbulence were not conducted with real phytoplankton cells, so more observational and laboratory data will be valuable for more accurate models.

Turbulence may enhance cell growth by increasing nutrient uptake and/or exposure to light. Sullivan et al. (2003) reported that growth rates of dinoflagellate species increased with turbulence levels up to $\varepsilon \approx 10^{-4}$ m^2 s^{-3}, but decreased at $\varepsilon \approx 10^{-3}$ m^2 s^{-3} although they still had fairly high growth rates. If we consider their result, the model may be improved by including a growth function that varies with cross-shore varying turbulence energy dissipation rates in the range of 10^0–10^{-5} m^2 s^{-3} (shoreline—surf zone edge). Also, the effect of turbulence on growth rate is species-specific as turbulence influences the growth rate of some species negatively (Peters and Marrasé, 2000), while others grow faster in turbulence (Davis et al., 1953; Savidge, 1981; Hondzo and Wüest, 2009). Moreover, the surf zone often receives nutrient-rich freshwater from land through the sand of the beach, and there may be spatial nutrient variability (i.e., the closer to shore, the higher in nutrients). In addition, the surf zone is a relatively shallow region, so generally phytoplankton are exposed to high irradiance, resulting in fast growth rates. Simulations of phytoplankton concentration can be improved by developing cell growth model with corresponding environmental variability.

Our DVM with depth-varying growth model was based on Talbot et al. (1990). This model case showed the most successful onshore phytoplankton migration in our simulations; however, it is not known whether this mechanism applies to any species. As mentioned previously, the ability to float by attaching to air bubbles has been observed in surf zone diatom species (Lewin and Schaefer, 1983), but offshore phytoplankton can also attach to bubbles. In fact, Shanks et al. (2018) collected foam from the sea surface in the rip current, and found that phytoplankton are often highly concentrated in the foam. Those phytoplankton consist of a lot of offshore diatoms and dinoflagellates, and a tiny percentage of surf zone species. It would have been interesting if they had determined the vertical distribution of phytoplankton and sampled at night like Talbot and Bate (1988a) performed.

The model can be improved in many aspects. It is necessary to collect species-specific information including habitat, growth rate, sinking and floating rates, cell size, and morphology. These parameters often interact with each other and the modeling is not trivial even for single species. If we consider that sand grains are sinking agent of phytoplankton, their size variability in the surf zone from observed data (e.g., Gallagher et al., 2011) and their dynamics from numerical model (e.g., Reniers et al., 2013) would help to improve the phytoplankton biophysical Lagrangian model. Likewise, if the target species interact with air bubbles, dynamics and size distributions of air bubbles produced by breaking waves in the surf zone from empirical data (e.g., Deane, 1997; Deane and Stokes, 1999, 2002) or numerical simulations (e.g., Ma et al., 2011) could be incorporated into the biophysical model. Air bubbles may be entrained by "obliquely descending eddies" (Nadaoka et al., 1989), which our model did not include. Another missing surf zone process in our model is a breaking wave roller (Feddersen, 2007; Reniers et al., 2013) that may entrain phytoplankton cells and transport them toward the shore. Moreover, wave conditions also influence onshore transport of plankton. Concentrations of phytoplankton in the surf zone at Sand City beach were higher between 0.5 and 1.0 m wave heights (Shanks et al., 2018). Most zooplankton concentrations in the surf zone tended to be negatively correlated with wave heights at Sand City beach (Morgan et al., 2017) and at a more reflective beach (Shanks et al., 2015; Fujimura et al., 2017; Morgan et al., 2017). Wave spectra may need to be applied for more realistic situations. Random wave groups generate infragravity waves and surf zone eddies that may add extra forcing to onshore transport of plankton and material within the surf zone (MacMahan et al., 2004; Reniers et al., 2010; Fujimura et al., 2014).

CONCLUSIONS

We found that both biological and physical parameters controlled onshore delivery of phytoplankton and the concentration of the cells in the surf zone. Both wave and wind forcing play an important role in phytoplankton transport. More modeled offshore phytoplankton cells tended to reach the surf zone in the diurnal wind cycle regime than that in the no-wind condition. The cells were highly concentrated in the rip channels by current convergence and rip circulations. Turbulence-induced growth and sinking enhanced the number of phytoplankton cells in the surf zone. DVM also facilitated onshore phytoplankton transport, and depth-varying growth increased the cell concentrations in the surf zone.

The model parameters could be improved with additional empirical data. Further investigation on dynamics of waves, currents, air bubbles, and sand grain will help to develop the model. Species-specific morphological, physiological, and behavioral characteristics of phytoplankton need to be studied as well. Once the model with necessary parameters is validated, it may be coupled with other ecological model such as NPZD and nested in a larger scale for more practical applications, including HAB predictions and fisheries management.

AUTHOR CONTRIBUTIONS

Designed the investigations: AF, AR, AS, JM, SM. Developed the model: AF, AR, CP. Performed the simulations and data analysis: AF. Prepared manuscript: All authors.

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REVIEW
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The Effects of Anthropogenic Stressors on Reproduction and Recruitment of Corals and Reef Organisms

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The persistence of populations of marine organisms depends on the success of the dual processes of reproduction and recruitment. The production of offspring alone is inconsequential unless larvae and propagules can recruit, which often entails a period of development and distribution in the water column and subsequent selection of appropriate habitats. For fish, this may mean drifting in currents before responding to particular habitat cues. For corals and other benthic invertebrates, larvae must undergo site selection, settlement and metamorphosis into the juvenile form, and survivorship is directly linked to site choice and environmental conditions. Both biotic and abiotic factors affect population replenishment success, and hence, anthropogenic influences such as pollution, sedimentation and climate change can negatively affect critical processes such as reproductive synchronization in spawning species, successful embryological development, appropriate site selection, settlement, metamorphosis and in the case of reef building corals, acquisition of the required zooxanthellae partner. Effective management practices are essential for ensuring the persistence of populations of coral reef organisms of economic, cultural and ecological value.

Keywords: corals, planulae, larval development, larval recruitment, pollution and global change, climate change impacts, metamorphic induction, anthropogenic stressors

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REPRODUCTION AND RECRUITMENT

Reproduction is the process by which new individuals are formed from parental stock, and can occur through asexual or sexual means. In corals, the most common type of asexual reproduction is via fragmentation, and often involves physical separation of a portion of the tissue-covered skeleton. This can occur as a result of fish feeding on associated crabs, shrimp, bivalves or barnacles, and the driver of recruitment "behavior" is gravity, that is, the fragment sinks, settles, attaches and hopefully survives. Other means of asexual reproduction can occur via tissue sloughing or polyp bail out, and the resulting ciliated tissue bits can disperse over greater distances and exhibit selective settlement behavior (Sammarco, 1982). Larvae can also be produced via parthenogenesis, and while genetically identical to the parent colony, exhibit classic larval behaviors. Sexual reproduction involves the fusion of sperm and egg (gametes) produced by the male and female of the species respectively. Sexual reproduction results in two opportunities for increasing genetic variability: one through the contributions of two different parents to the offspring and another through the "crossing over" among chromosomes that occurs during the prophase one stage of meiosis, the reduction division that makes haploid (1n) gametes that fuse to become a diploid (2n) organism. No matter how the progeny are formed, they do not contribute to the population unless they successfully recruit, and that is where behavior comes in.

The persistence of populations depends on the success of both reproduction and recruitment processes. With a focus on the importance of larval behavior for successful recruitment, the following discussion will center on sexual reproduction as the primary means of producing this critical life history stage for the perpetuation of coral reefs and related ecosystems. There are six chemically mediated steps involved in the replenishment of reef populations: gamete development within mature coral colonies, synchronization of gamete release, successful fertilization of eggs by sperm, complete embryological development to the competent larval stage, settlement and metamorphic induction, and acquisition of symbiotic zooxanthellae in recruits that do not have them vertically transmitted by the parent colony (Richmond, 2014; **Figure 1**). These key processes are affected by both density dependent and density independent factors.

As with all sessile and benthic organisms, for reproductive events to be successful in the production of viable larvae, a critical density of parental stock is required. As the distance between individuals and colonies of the same species increases, the incidence of appropriate egg-sperm interactions decreases, with reduced levels of fertilization and larval production. This is called the Allee Effect, and is well known within marine organisms (Gascoigne and Lipcius, 2004). Population density is a function of environmental conditions, stressors and disturbance.

Water and bottom quality are essential parameters that affect the health of coral reefs and other marine ecosystems. Reduced water quality can stress adult populations, inhibiting gametogenesis and reducing chemical signaling between conspecifics that helps with the synchronization of spawning, the viability of gametes, fertilization success and the ability of embryos to develop into viable planula larvae. As gametes (egg and sperm) are among the most sensitive life history stages to environmental parameters, terrigenous runoff is a serious problem that impacts reproduction of marine organisms (Richmond, 1993). Bottom quality affects recruitment success in corals and many other benthic invertebrates. Sediment cover prevents larvae from sensing key settlement cues, both chemical and textural, from preferred substrata such as crustose coralline algae. Larval metamorphic induction may be prevented by sediment and algal cover through substrate instability, the alteration of the benthic microbiome, and the alteration of bottom chemistry. In addition to the local stressors mentioned above, increased temperatures and ocean acidification tied to global climate change are factors that also affect reproduction and recruitment in a broad range of marine organisms. These anthropogenic issues will be discussed below.

FIGURE 1 | Recent coral recruit exhibiting colony growth through extra-tentacular budding and the acquisition of symbiotic zooxanthellae from the ambient environment.

LARVAL COMPETENCY

The competency period of larvae, the time during which they can successfully disperse, settle and metamorphose, is an important determinant of connectivity among sites and populations. The longer the competency period, the greater the distributional range of a species, and broader distributions translate into enhanced survival of species exposed to local and global level stressors with the associated threat of local extinction. The competency period of larvae is tied to nutritional mode and energy availability. Planktotrophic larvae actively feed, and often have specific structures that aid in food capture. They have a delay before they can recruit, the pre-competency period, during which time they undergo additional development and often, morphological changes. Lecithotrophic larvae survive primarily on stored energy reserves, such as lipids provided in the eggs. The term mixotrophic refers to larvae that use a combination of stored energy reserves and planktonic feeding, which can include absorption of dissolved nutrients, and in the case of corals, translocated metabolites from symbiotic zooxanthallae.

While in the plankton, larvae are not limited to drifting at the mercy of currents, but can exert a degree of control through vertical and horizontal swimming behaviors. Such movement can change the water parcels in which the larvae are contained and hence, the direction and speed of travel, ambient temperature that affects larval development and metabolic rates, and light levels including photosynthetically active radiation (PAR) and UV exposure. An extreme example is for larvae that get entrained in water parcels affected by the Kelvin Wave associated with the onset of El Nino conditions. Such larvae can be transported over hundreds to thousands of km over a period of weeks to months (Richmond, 1990). Downward vertical movement of larvae can also affect entrainment of larvae in bottom currents and eddies that enhances recruitment on coral reefs and other benthic habitats. Recent research has demonstrated that larval swimming behavior can be influenced by a number of parameters including light, gradients of salinity and temperature, as well as by auditory and chemical cues. Both fish and invertebrate larvae have been documented to respond to reef sounds that aid in the recruitment of larvae to reefs, and chemical cues can influence larval swimming and settlement behavior (Vermeij et al., 2010). While both auditory and chemical cues can attract larvae, the distance over which some, including coral planulae, can swim is limited (Figueiredo et al., 2014; Hata et al., 2017).

Fish larvae usually have an initial distribution pattern tied to currents, but after a degree of development and spinal hardening, can begin to exhibit directional swimming. Coral reef fish, as opposed to pelagic species, need to find specific habitats in order to recruit, grow and eventually reproduce, hence, cueing behavior is of paramount importance. Specific cues include sounds and smells. Waves impacting reefs and other barriers send sounds over relatively long distances. Interestingly, these reflections and refractions of wave energy are also used by traditional navigators in the Pacific Islands to identify the location of landmasses and submerged features. Over shorter distances, the sounds of crabs, snapping shrimp and fish can help larvae navigate toward healthy reefs. Dead reefs and reefs in decline may provide fewer cues to which larvae can respond (Dixson et al., 2014). The natural chemistry of reefs, tied to everything from coral mucus, algae and bacteria, also provides signals to larvae, which possess chemoreceptors. Toxicants that block these chemical signals or the larval receptors, act to impede recruitment (Peters et al., 1997).

Coral planula larvae do not randomly settle and metamorphose, but rather, select their recruitment sites (Golbuu and Richmond, 2007). Bacteria have been specifically identified as important cues for coral larval recruitment to specific substrata. Coral planulae have been found to also respond to specific crustose coralline algae (CCA), likely due to associated polysacchides and glycoglycerolipids (Tebben et al., 2015; **Figure 2**).

Coral larvae from brooding species and some spawning species (e.g., *Montipora*) possess symbiotic zooxanthellae that are vertically transmitted from the parent colony. These algal cells provide additional energetic input to the larvae and can extend the competency period (Richmond, 1987). While the period during which these larvae can successfully settle and metamorphose can extend from weeks to months, translating into the potential for long-distance dispersal, studies have shown that most larvae travel over short distances and many reefs are self-seeding (Sammarco et al., 1989; Jones et al., 1999; Figueiredo et al., 2013). This is due to a combination of abiotic factors (currents and associated eddies) and larval behavior, including cueing to the biotic factors of natal reefs, identified above.

Water quality remains a key concern during the planktonic phase of larvae throughout the competency period. Substratum quality is also important for settlement and metamorphosis to occur. The implications are that efforts to protect bottom and water quality in and around coral reef ecosystems are of critical importance to maintaining reef populations by supporting successful reproduction and larval recruitment.

THE EFFECTS OF STRESSORS ON CORAL REPRODUCTION AND RECRUITMENT

Water Quality

The world's nearshore marine habitats are being increasingly exposed to a variety of anthropogenic stressors, such as sedimentation, eutrophication, pollution, and overfishing (Morgan et al., 2016), all of which have a profound impact on reproduction, recruitment and survival of larvae. As mentioned above, early life stages of many marine organisms are more sensitive to pollutants than adult stages (Reichelt-Brushett and Harrison, 1999), due in part to the important role that chemical cues play in substrate selection and metamorphosis of larvae in many marine organisms (Hadfield and Paul, 2001; Freckelton et al., 2017). For example, many species of coral larvae use chemical cues to settle on a substratum where specific coralline algae and/or their associated bacteria are present (Golbuu and Richmond, 2007; Vermeij et al., 2008; Tebben et al., 2015). Recently, a single bacterial metabolite, tetrabromopyrrole, was shown to induce metamorphosis in certain coral species, occurring even without attachment to a substratum (Tebben et al., 2011; Sneed et al., 2014). Chemical pollutants, therefore, affect key life stages and behaviors of corals and other marine organisms by interfering with their chemosensory functions.

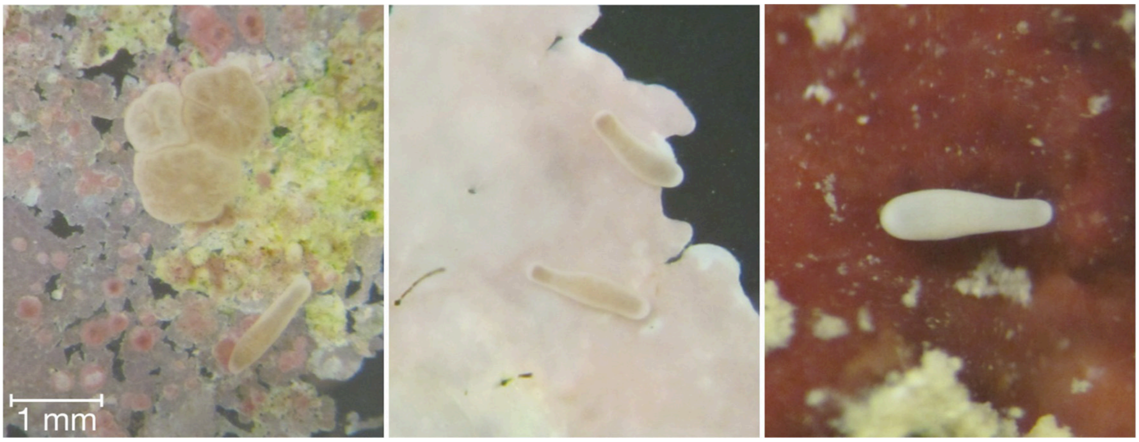

FIGURE 2 | Coral planulae undergoing settlement and metamorphosis (panel 1) following exploration of the substrata (panels 2 and 3) and encountering the proper chemical/biotic cues.

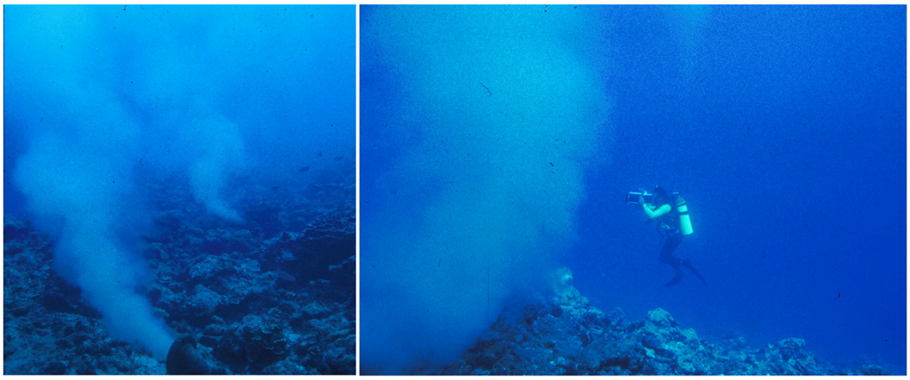

FIGURE 3 | Sewage discharges along a reef on Guam, resulting in decreased recruitment of coral larvae. The freshwater effluent rises 100% of the time and bathes the adjacent shallow water reef area when there is an onshore wind. The chemical content includes personal care products, heavy metals, pesticides, pharmaceuticals, hydrocarbons and even estrogenic compounds from un-metabolized birth control pills.

A variety of chemical agents are introduced into our coastal waters via coastal development, terrestrial runoff, sewage outfalls and toxic antifouling paints from ships (**Figure 3**). Many studies have shown the negative effects of these agents on coral larvae and their behaviors (Woods et al., 2016). For example, increased heavy metal concentrations reduce fertilization rates, larval survival, settlement success, metamorphosis, and growth rates of reef-building corals. Copper (Cu) is shown to affect all of the above stages in coral larvae at relatively low concentrations (Reichelt-Brushett and Harrison, 1999, 2000; Victor and Richmond, 2005; Negri and Hoogenboom, 2011). In fact, Cu inhibits the metamorphosis of coral larvae at the lowest concentration of any metals tested so far (Reichelt-Brushett and Harrison, 1999). Exposure to iron (Fe) induced oxidative stress responses and DNA damage in coral larvae (Vijayavel et al., 2012), affecting their metabolic functions and behaviors. Exposure of coral larvae to mercury, cadmium and zinc showed neutral or mixed results (Heyward, 1988; Reichelt-Brushett and Harrison, 1999, 2005; Farina et al., 2008), suggesting interspecific differences in sensitivity to these metals.

The effects of organic compounds such as anti-fouling agents, hydrocarbons, and pesticides have been increasingly studied in marine organisms, including their impacts on reproductive and larval recruitment success. Tributylin (TBT) and Irgarol 1051 are active compounds of anti-fouling paints, and are reported to inhibit larval settlement and/or metamorphosis (Negri et al., 2002; Inoue, 2004; Negri and Marshall, 2009; Knutson et al., 2011). Since the banning of applying paints with TBT in 2003 by the International Maritime Organization, the use of the algaecide Irgarol in marine paints has increased dramatically. However, even relatively small concentrations of Irgarol can inhibit coral larval settlement (Knutson et al., 2011), which suggests that the Irgarol use may need to be reevaluated. Hydrocarbons, such as crude oil, dispersed oil, oil dispersant, and benzo[a]pyrene, are all reported to negatively affect fertilization, metamorphosis, and settlement of coral larvae (Epstein et al., 2000; Lane and Harrison, 2000; Negri and Heyward, 2000; Goodbody-Gringley et al., 2013). Oil dispersants and dispersed oil appear to have more negative effects than crude oil itself (i.e., water soluble fractions); morphological deformations and loss of normal swimming behavior of coral larvae were observed with exposure to dispersants and dispersed oil (Epstein et al., 2000).

Corals are holobionts, harboring endosymbiotic algae, zooxanthellae (*Symbiodinium* spp.), in their tissues. These algal symbionts provide the majority of the coral's energy needs through photosynthesis. Increased detection of herbicides and insecticides in marine environments has raised serious concerns regarding their impacts on coastal coral reef ecosystems (Markey et al., 2007; van Dam et al., 2011), since some herbicides used in agriculture and antifouling paints, such as diuron and atrazine, are photosystem II (PSII) inhibitors that directly affect zooxanthellae's functions (Owen et al., 2002; Jones et al., 2003; Jones, 2004, 2005). Our understanding about how these herbicides and insecticides affect coral hosts is still limited. The effects of pesticides found in coastal waters, on coral reproduction and physiology, are of high concern to resource managers. Our results from laboratory exposure experiments showed that the tested herbicides and insecticides had negative effects on at least one or more of coral life stages. For example, Roundup® (Monsanto Company) significantly reduced fertilization and settlement rates in corals at very low concentrations (0.0069 ppm), and caused damage to eggs at a relatively low concentration (>0.35 ppm) (Diu, 2016). Another emerging pollutant gaining attention in the marine environment is the active ingredient in some sunscreens, oxybenzone. Increased mortality, deformation, and DNA damage, as well as reductions in photosynthetic efficiency were observed in coral larvae exposed to oxybenzone (Downs et al., 2016). These observations raise concerns about the environmental safety of other personal care products that enter into coastal waters and the open ocean.

Bottom Quality

Water and substratum quality are critical components affecting both reproduction and recruitment of marine organisms. In order for successful population replenishment to occur, consideration must be given to the source areas, the conduits of connectivity and the recipient sites. For example, larvae formed at one site will be physiologically compromised or killed if transported across an area affected by polluted and sediment-laden watershed discharges (Victor et al., 2006). Even a drop in salinity will affect survivorship of many types of larvae, including corals and echinoderms (Richmond and Jokiel, 1984). Contaminated recipient sites and those with accumulated sediment will also be inhospitable to benthic invertebrate and fish larvae from clean source sites, as such degradation will affect critical chemically cueing.

Sedimentation affects the success of reproduction and recruitment several different ways. During spawning events, sediment, particularly the finer clay-size particles, can adhere to eggs, causing them to sink rather than float to the ocean's surface, where fertilization often occurs. Sediment is a major carrier of toxicants from land to the sea, where the change in chemistry can cause contaminant release (**Figure 4**). Such pollutants include petroleum products (polycyclic aromatic hydrocarbons–PAH's), pesticides (both insecticides and herbicides), personal care products and heavy metals. Sediment particles often serve as nuclei that aggregate organic material, including mucus and phytoplankton, which harbor bacteria, and when this material sinks to the bottom, it increases biological oxygen demand (BOD), dropping both oxygen levels and pH at the sediment-water interface (Wolanski et al., 2003). This effect can negatively impact the survivorship and growth of larval recruits. Finally, sediment blocks key metamorphic inducers needed by many types of larvae, and most benthic epifaunal larvae cannot recruit to such unstable substrata.

Sediments impact reproductive, larval behavior and recruitment success. In additional to the chemical effects listed above, sediment has physical effects that in turn, affect the physiology of organisms. For organisms dependent upon photosynthesis for energy, metabolism, growth and reproductive allocation, the shading effects of sediment block photosynthetically active radiation (PAR) that is essential to running the light-mediated chemical reactions. Turbidity, expressed as a weight per unit volume of water (e.g., mg/l), is especially problematic for photosynthesis. Sedimentation deposition rate, a weight per unit area over a given time period (e.g., g/m^2/day) impacts both photosynthesis and energetics, due to the cost of shedding particles. Sediment can be re-suspended numerous times, so even without the addition of new materials from land-based sources, waves can result in additional impacts through reintroducing particles into the water column.

Temperature

Coral larvae remain viable and competent within the ambient temperature range of the parent colonies (Woolsey et al., 2015). As with adult colonies, deviations of a few degrees above or below the norm can have deleterious effects, such as reducing competency or inducing mortality. The expected increase in tropical and subtropical seawater temperatures of 2–4°C due to climate change, has major implications for coral larval survival, development, dispersal, and settlement (IPCC, 2007). Temperature is tied to larval development, and alterations in the ambient rearing temperature can have drastic effects. Abnormalities in embryogenisis of the spawning coral *Acropora millepora* were seen at 32°C (4°C above ambient temperature where gametes where collected), as well as decreased fertilization rates, with no fertilization occurring at 34°C (Negri et al., 2007). A temperature increase reduced pre-competency periods by as much as an entire day in some coral species, which can affect the dispersal range for coral species, as well as impede the ability for devastated coral reefs to recruit new individuals and recover following bleaching events (Heyward and Negri, 2010). Model predictions suggest that increasing temperatures will serve to increase local retention of coral planulae due to reduced competency periods, and reduce connectivity among reefs separated by greater distances (Figueiredo et al., 2014). The implications are positive for locally targeted conservation efforts but raise additional concerns for reefs and populations dependent on external larval supplies for recovery and enhancing genotypic diversity.

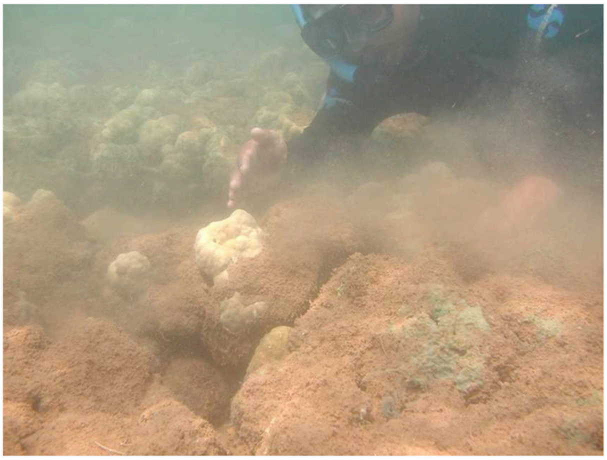

FIGURE 4 | Sediment covering the reef surface blocks metamorphic inducers and prevents larval recruitment.

Elevated temperature effects on coral planulae can have regional implications for population replenishment as well as global ones, as higher latitude larvae tend to develop more slowly than their tropical counterparts. An increase of even a single degree (°C) above the normal range can increase the metabolic expenditure of stored energy, increasing premature metamorphosis and reducing recruitment success in addition to causing outright mortality (Edmunds et al., 2001; Graham et al., 2017). In aposymbiotic larvae from *Diploria strigosa,* a 2°C rise in temperature from an ambient 28°C seawater temp caused 50% mortality, and an increase to 31°C caused 70% mortality (Bassim and Sammarco, 2003).

As mentioned, coral larvae respond to different chemical and biological cues, and must have an appropriate settlement substrate for successful settlement and metamorphosis to occur. Temperature experiments elevating seawater to 32°C for a period of a week have been able to bleach CCA, also resulting in a shift in its microbial community (Webster et al., 2010). *Acropora* *millepora* larval settlement and metamorphosis was reduced by 50% when these planulae were exposed to bleached CCA compared to healthy CCA from ambient seawater conditions. While a microbial shift can occur by altering the chemical compounds released by CCA, it's also important to note that the color change from pink to white when CCA bleaches can also alter larvae settlement due to a resulting lack of an appropriate spectral cue. In an experiment examining synthetic surfaces of either white or red hues, the coral larvae preferred a red surface 85% more often when compared to a white synthetic surface when both were also exposed to a chemical cue (Foster and Gilmour, 2016). The larvae themselves exhibit spectral variance by producing fluorescent proteins that change in response to environmental conditions. Fluorescent proteins are present in both larval and adult corals. While their function is not fully understood, they appear to be altered when the animal is exposed to stressors (Palmer et al., 2009). There is a demonstrated change in the expression of green fluorescent protein (GFP) in response to increased light, as well as red fluorescent protein (RFP) in response to heat(Rodriguez-Lanetty et al., 2009; Kenkel et al., 2011). The combined effect of increased water temperature and light intensity can also affect larval settlement, with a 16% decrease in larval settlement when they are exposed to both high temperatures and higher than normal light conditions (Kenkel et al., 2011).

When considering larval survival and physiology under increased temperatures, the symbiotic relationship between the animal and algal symbionts must be considered. Aposymbiotic larvae and symbiotic larvae both respond to stress in different ways, yet survivorship between temperatures of 28–32°C is not significantly different (Baird et al., 2006). When the aposymbiotic larvae from *A. millepora* were exposed to temperatures above their normal range for a period of 10 h, heat shock protein gene expression was elevated but oxidative stress pathways remained unchanged (Rodriguez-Lanetty et al., 2009). The infection of symbionts within aposymbiotic larvae is a complex process that is just beginning to be understood under normal seawater temperatures, and may be altered under increased seawater temperatures (Weis et al., 2001). A study examining physiological responses to 4 clades of symbionts, as well as coral larvae infection, found that there were different optimum temperatures among the symbiont types where they had the ability to infect aposymbiotic coral larvae (Baird et al., 2008). Certain symbionts demonstrated lower rates of survival even at 32°C, giving other symbiodinium strains a competitive edge. This advantage may come with tradeoffs however, as one of the most thermally tolerant strains had the slowest rate of population increase after infecting the coral larval host. This could have long-term impacts on the ability for the coral recruit to establish itself and grow, when fewer symbionts are available to provide nutrients needed for growth.

The means by which corals transmit their symbionts can affect stress in and survivorship of larvae. Hartmann et al. (2017) suggested that vertical transmission of zooxanthellae to coral eggs may exact a cost on gamete and larval survival due to the effect of increased buoyancy from lipids that result in the exposure to increased temperature and UV light at the sea surface. As many corals spawn during the rainy season in parts of the world, the sea surface can be a stressful environment with reduced salinity and increased toxicant concentrations from freshwater runoff. Hartmann et al. propose that the acquisition of symbionts after metamorphosis improves fertilization and out-crossing following spawning. The adaptive advantage of horizontal transmission of zooxanthellae is reflected in the fact that the majority of spawning corals (71%) acquire their symbionts that way.

Under conditions of elevated temperature, algal symbionts can contribute to stress and mortality in coral larvae. Yakovleva et al. (2009) found coral planulae with zooxanthellae had higher mortality rates than those lacking algal symbionts at high temperatures. Mortality was attributed to oxidative damage tied to photosynthesis and was a function of both the magnitude of increased temperature and the duration of exposure. As with exposure to other physical and chemical stressors, zooxanthellae shift from being a mutualistic partner to becoming a burden at higher temperatures.

Ocean Acidifcation

Reduced oceanic pH attributed to increasing levels of atmospheric CO_2 is a concern for the future of coral reefs as the structural foundation of these ecosystems results from the deposition of $CaCO_3$ (aragonite). Chua et al. (2013), performed a study of the effects of pH on coral planulae using four relevant exposure treatments, and found no consistent effects on embryological development, larval survivorship and metamorphosis. They posit that larvae containing zooxanthellae may be more sensitive to the effects of decreased pH through metabolic effects on the symbionts. As coral planulae (generally) do not calcify while in the plankton, ocean acidification is more likely to directly affect larvae that do, such as those of sea urchins (Kurihara, 2008). However, the long-term effects of OA on coral recruitment and survivorship are expected to increase and, based on current predictions, be substantial. Reduced pH does affect the recruitment and growth of crustose coralline algae, which has been shown to be a preferred settlement substratum for many coral species (Kuffner et al., 2008). As small coral recruits can be outcompeted for space by a number of benthic organisms including algae, sponges and ascidians, reduced colony growth rates will affect survivorship as OA increases.

SURVIVORSHIP–SELECTION/ADAPTATION VS. ACCLIMATIZATION

Intraspecific variation, or inter-individual differences, in traits arise from genetic predispositions, past experiences and physiological states (Guest et al., 2012; Nanninga and Berumen, 2014), and is increasingly recognized as an important ecological factor that affects population dynamics and evolution of species, including reproductive success (Benton et al., 2006; Bolnick et al., 2011). In reef-building corals, significant differences in larval success has been observed among different genotypes (Meyer et al., 2009; Baums et al., 2013; Miller, 2014; Miller et al., 2016), as well as due to the parental experiences of exposure to stressful conditions (Putnam and Gates, 2015). This tells us that the larval stages are subject to strong selective pressures from their environmental conditions. Since persistence of populations, and ultimately species, depends on producing better adapted genotypes, the larval stages play a key role in coral population dynamics, connectivity, and survival. The fitness of existing individuals depends on their acclimatization potential, and many larval behaviors likely contribute to increasing their fitness; examples include selecting an optimal environment to settle (e.g., Davies et al., 2014; Dixson et al., 2014; Doropoulos et al., 2016), using reverse metamorphosis to escape from adverse conditions (Richmond, 1985; Negri et al., 2005), and potentially benefitting from increased size by forming a chimeric aggregate (Amar et al., 2008). When selective pressures exceed the acclimatization capacity of an individual, the individual will be eliminated from the population (i.e., selection). However, since no individual larva will experience exactly the same conditions, one evolutionary response is to produce genetically variable offspring so that the population will have enough adaptive capacity to respond to environmental heterogeneity and unpredictability. Intraspecific variation in reproductive success may, therefore, be a result of such an evolutionary strategy. Looking forward, corals and many other marine organisms will face strong selective forces from rising sea surface temperatures and ocean acidification (Webster et al., 2013; Baums et al., 2014). The larval stages known to be vulnerable to environmental stressors (Polato et al., 2010) will especially be subject to this strong selection, resulting in adaptation playing an essential role in how coral populations respond to changing environmental conditions. Standing genetic variation fuels such short-term adaptation (Stapley et al., 2010; Voolstra et al., 2011; Shinzato et al., 2012). In this regard, loss of genetic diversity already seen in some threatened coral populations (Baums et al., 2013) poses a great concern, as it reduces the coral's future reproductive and adaptive capacity. Human activities, including those responsible for global climate change, are predicted to reduce overall genetic diversity in populations and species (Templeton et al., 2001; Pauls et al., 2013), which further threatens the persistence of coral reef ecosystems.

SUMMARY AND CONCLUSIONS

In a world of mounting anthropogenic stressors affecting the world's oceans and all life contained within, the ability of populations of organisms to survive, reproduce, evolve and grow is threatened at the local, regional and global levels. An understanding of the reproductive and recruitment behavior of marine organisms is essential to addressing the challenges of resource sustainability through responsive and effective management of the human activities responsible for resource declines. New tools such as genomics, proteomics and transcriptomics allow for the study of behaviors at the cellular and molecular levels, which when combined with more traditional studies of physiology and organismal behavior, have the potential to provide key guidance. The needs are pressing if there is to be a sound legacy of ocean resources for future generations.

AUTHOR CONTRIBUTIONS

RR organized the manuscript, coordinated sections with the coauthors, wrote several sections, provided figures and edited versions. KT wrote several sections and edited versions. NS wrote several sections, contributed figures and edited versions.

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Biophysical Simulations Support Schooling Behavior of Fish Larvae Throughout Ontogeny

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Schooling is very common in adult and juvenile fish, but has been rarely studied during the larval stage. Recent otolith micro-chemistry studies of coral reef fish have demonstrated that cohorts of larvae can move through similar paths and settle within a few meters one from another. However, little is known about the processes involved in the formation and maintenance of these cohorts. Here we use a biophysical modeling approach to examine whether local hydrodynamics, various individual behaviors, or larval schooling can explain cohesive patterns observed for *Neopomacentrus miryae* in the Gulf of Aqaba/Eilat (Red Sea), and whether schooling is feasible in terms of initial encounter probability and cohesiveness maintenance. We then examine the consequences of schooling behavior on larval settlement success and connectivity. Our results indicate that: (1) Schooling behavior is necessary for generating cohesive dispersal patterns, (2) Initial larval encounter of newly-hatched larvae is plausible, depending mainly on initial larval densities and patchiness, and (3) schooling behavior increases the rate of larval settlement while decreasing the percentage of realized connections. Together with mounting evidence of cohesive dispersal, this numerical study demonstrates that larval schooling throughout the pelagic phase is realistic, and has a significant effect on settlement success and connectivity patterns. Future research is needed to understand the mechanisms of fission-fusion dynamics of larval cohorts and their effect on dispersal. Our findings should be considered in future efforts of larval dispersal models, specifically in the context of marine connectivity and the planning of marine protected area networks.

Keywords: larval dispersal, schooling, cohorts, coral reef fish larvae, cohesive dispersal, settlement, connectivity, Gulf of Aqaba/Eilat

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INTRODUCTION

Adult and juvenile fish often swim in groups. Such schooling behavior can help reduce drag and conserve energy (Weihs, 1975), improve orientation (Codling et al., 2007), reduce the risk of predation (Shaw, 1978), and enhance the detection of food and mates (Shaw, 1978). On the other hand, schooling fish may suffer higher mortality and lower growth rates due to competition within the group (Hixon and Jones, 2005). The prevalence of schooling suggests that the overall balance would seem to be positive (Shaw, 1978).

The advantages of schooling may similarly benefit the pelagic larval phase that characterizes the life-cycle of most coral reef fishes (Leis, 2006). These larvae are thought to actively group, mainly during late larval stages, once their sensory and movement capacities have matured enough to support this behavior (Shaw, 1978; Arvedlund and Kavanagh, 2009). Specifically, larval schooling may be similar to adult fish schooling, where collective behavior emerges from simple "individual-fish" rules based on the location of the nearest neighbor/s (Couzin et al., 2002).

Little is known about the frequency of schooling behavior across species and its ontogenetic dynamics. Previous studies indicated that *Aldrichetta forsteri* and *Gobiosoma boscifish* larvae school at early stages when their size is ∼5 mm and their fins are not fully developed yet (Breitburg, 1991; Kingsford and Tricklebank, 1991). However schooling was also reported at later larval and post-larval stages for different species (reviewed in Leis, 2006).

Mounting evidence, derived from the analysis of otolith micro-chemistry (Ben-Tzvi et al., 2012; Shima and Swearer, 2016) and genetic relatedness (Bernardi et al., 2012; Selwyn et al., 2016), suggests that cohorts of coastal marine fish may be sharing a substantial portion of their dispersal histories (by "cohort" we mean a group of larvae of same age). While it is tempting to relate these patterns to larval behavior, they may also result from aggregation by prevailing hydrological features and/or local cohesive Lagrangian structures (Siegel et al., 2008). The relative contribution of biological, physical, and bio-physical processes to the generation and maintenance of such cohesive dispersal pattern, i.e., shared dispersal paths among individuals within the same cohort, is largely unexplored.

This gap of knowledge is critical, given the demographic and ecological ramifications of the dispersive fate of marine larvae (Levin, 2006). Specifically, the dispersal outcome of schooling larvae is likely to differ from individual larvae as larval schools are characterized by faster swimming speeds, and higher precision of orientation (Irisson et al., 2015). Distinguishing between individual and schooling dispersal is important since dispersal and connectivity are central elements affecting population dynamics, and are often considered when designing marine protected areas networks (Cowen and Sponaugle, 2009). Additional importance of larval schooling lies in its potential effect on the ecology of pelagic ecosystems via planktonic predator-prey dynamics (McGurk, 1986; Frank et al., 1993; Bradbury et al., 2003), planktonic patchiness enhancement (Bradbury et al., 2003), species diversity (Hill, 1973).

In the current study we used a biophysical model of the Gulf of Aqaba (GoA) to test which aspect of larval behavior is necessary and sufficient to reproduce patterns of cohesive dispersal reported for *Neopomacentrus miryae* in the GoA (Ben-Tzvi et al., 2012). Briefly, Ben-Tzvi et al. (2012) have demonstrated that newly settled *N. miryae* cohorts shared a highly similar otolith micro-chemistry pattern within each cohort compared to between cohorts. In the current study, we tested whether different scenarios generate cohesive cohorts by examining passive drift, as well as by invoking larval behaviors such as simple random walk (SRW), auto-correlated directional swimming (CRW; Berenshtein et al., 2017), ontogenetic vertical migration (OVM; Paris and Cowen, 2004; Irisson et al., 2010; Huebert et al., 2011), biased correlated directional swimming (BCRW; Staaterman et al., 2012; Mouritsen et al., 2013), and schooling behavior (Irisson et al., 2015). We then examined the plausibility of larval encounter during the early pelagic phase; their capacity to overcome turbulent velocities and remain grouped; and finally, we quantified the relative changes in settlement-success and connectivity in schooling vs. non-schooling dispersal.

METHODS

Study Site

The Gulf of Aqaba is a semi-enclosed elongated extension of the Red Sea (**Figure 1A**), stretching across ∼180 km (**Figure 1B**), with maximal width and depth of ∼27 km and 1,850 m respectively. The GoA circulation is characterized by deep mixing during winter (Feb-March), and stratification during the rest of the year, with a strong density-driven exchange flow with the Red sea during April–August (Biton and Gildor, 2011). The GoA circulation is also dominated by a chain of several sub-meso-scale eddies along its main axis (Biton and Gildor, 2011).

Study Fish

Neopomacentrus miryae is endemic to the Red Sea and is highly abundant in the GoA. The ecology of this species was described by Fishelson et al. (1974) referring to it as *Abudefduf azysron* (Dor and Allen, 1974). Adult *N. miryae* are planktivorous, found in large stationary schools along vertical walls of forereefs, with males guarding and aerating demersal eggs. *N. miryae* spawning season spans between November-May, and larvae are found at depths of 0-100 m in the water column, with highest abundance at the top 25 m (Kimmerling et al., 2017).

Biophysical Model of the GoA

The biophysical model of the GoA (Berenshtein et al., 2017) was composed of 3 parts: First, the winds at 10 m above sea level were computed using an atmospheric model- Weather Research and Forecasting model (WRF; Skamarock et al., 2001), Next, wind data was used to force a 3D high resolution oceanographic model- Massachusetts Institute of Technology general circulation model (MITgcm; Marshall et al., 1997), Finally, an offline particle tracking algorithm (modified from Fredj et al., 2016) made use of the 3D circulation data combined with larval biological traits to compute larval trajectories. The resolution of the MITgcm data was of 1 h (temporal), 300 m (horizontal), and 32 depth layers most of which were concentrated in the upper 300 m (Biton and Gildor, 2011; Berenshtein et al., 2017). The temporal resolution of the particle tracking model was of 10 min (time-step length), with a spatial resolution of centimeters due to a continuous 3D grid, and spatial interpolation of larval positions. The detailed description of the model can be found in Berenshtein et al. (2017).

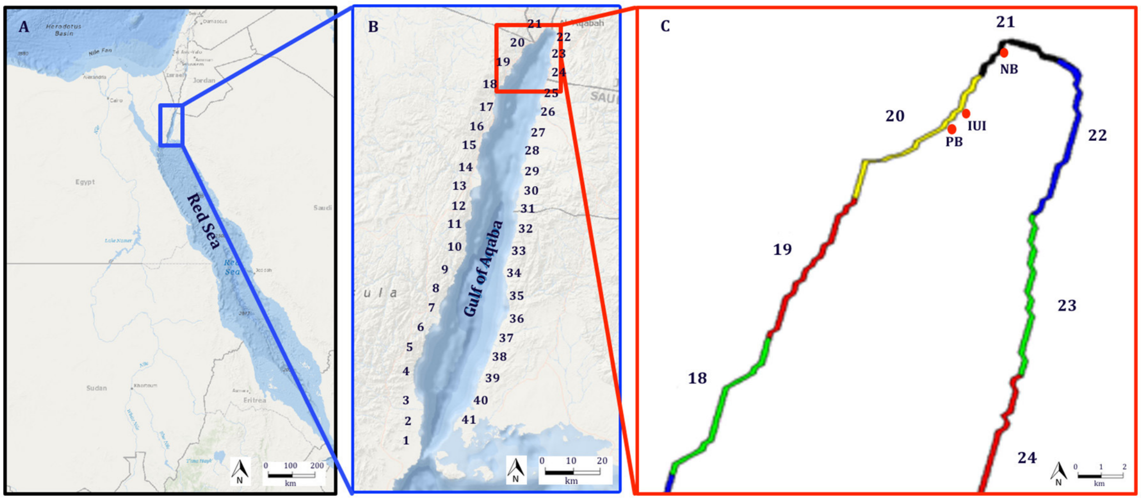

FIGURE 1 | Study area: **(A)** The Red Sea, and **(B)** The Gulf of Aqaba (GoA). Numbers in **(B)** represents the 41 reef polygons which are used in the biophysical model. **(C)** Cohort recruitment sites in the northern GoA: Princess Beach (PB), Inter-University Institute (IUI), and the North Beach (NB).

Backward and Forward-in-Time Passive Simulations

For our simulations we used 5 real recruitment events which occurred at 3 sites in the northwestern coast of the GoA: North Beach (NB), Inter-University Institute (IUI), and Princess Beach (PB) (**Figure 1C**; Ben-Tzvi et al., 2012). In Ben-Tzvi et al. (2012), newly-recruited fish were collected with hand-nets, and their age and day of recruitment was determined using otolith analysis. Newly-recruited fish that shared the same site, age and recruitment day were considered of the same cohort (Ben-Tzvi et al., 2012).

To examine whether the local hydrodynamics (advection and turbulence) could generate patterns of cohort cohesiveness similar to those observed in *N. miryae* (Ben-Tzvi et al., 2012), we performed backward and forward-in-time simulations using the dates and locations of the collected cohorts and their estimated PLDs (**Figure 2C**; Ben-Tzvi et al., 2012).

The rational of this approach was that if currents were to generate a cohesive dispersal pattern, they would have to be sufficiently strong and persistent to overcome the system's stochasticity. Such pattern would result in similar trajectories in backward and forward-in-time simulations, connecting between the settlement sites, and the hatching locations on the reef.

In the backtracking simulation (Sim. #1, **Table 1**) 5,000 passive virtual larvae were released from each of the recruitment sites at their corresponding dates. In the forward simulation (Sim. #2, **Table 1**), 20 virtual larvae were released from each of the locations of virtual larvae which ended up on the reef in the backtracking simulation, releasing a total of 4,480 virtual larvae (Sim. #2, **Table 1**).

We then visually examined the simulated trajectories for indication of cohort-unique dispersal trajectories, imposed solely by local hydrodynamics.

Pairwise Distances and Probability of Adjacent Settlement

To determine if various larval behaviors can generate the observed cohesive dispersal pattern we released pairs of virtual larvae from the entire fringing reef of the GoA (41 reef polygons in **Figure 1B**) and tracked them forward in time (Sim. #3–8, **Table 1**). For each simulation, 1,000 pairs of larvae, characterized by identical hatching times and locations, were released daily at midnight across 9 release days (15th—23th of March 2004). Larval trajectories were computed in the biophysical model according to advection, turbulence, and larval behavior (Berenshtein et al., 2017). Mortality was not applied in the biophysical simulations.

To quantitatively assess the occurrence of cohesive dispersal we computed: (1) larval pairwise distances, i.e., the distance separating paired virtual larvae across the PLD, and (2) the probability of sampling 2 settled nearest neighbors, which hatched at the same location and time. While the former corresponds to the observed similarity in larval paths deducted from the trace-element of otolith rings, the latter corresponds to the similarity in the site of origin deducted from the trace-element of otolith cores (Ben-Tzvi et al., 2012).

Since very little is known about the behavior of *N. miryae* larvae, we chose to apply the commonly observed and modeled larval behaviors for other species within the Pomacentridae family (Leis and Carson-Ewart, 2003; Irisson et al., 2009, 2015; Mouritsen et al., 2013; Berenshtein et al., 2014). Behaviors, which include movement toward a common direction (e.g., OVM and BCRW), are expected to produce convergence of larval paths, which would be expressed in reduced pairwise distances compared to passive simulations. The following behavioral scenarios were implemented (Sim. #3–8, **Table 1**).

TABLE 1 | Biophysical simulations scenarios- model configuration and behavior of virtual larvae.

Simulation	Domain	Release areas	Direction in time	Time of release	Number of virtual larvae released	Behavior
1	GoA	Sample locations are in **Figure 1C**	Backward	12:00 according to the date of settlement	25,000	Passive
2	GoA	Virtual larvae that ended up on the reef in the backward simulation. See **Figure 2B**	Forward	15–23/3/2004	4,880	Passive
3	GoA	Reef polygons (Berenshtein et al., 2017)	Forward	15–23/3/2004	32,046	Passive
4	GoA	Reef polygons (Berenshtein et al., 2017)	Forward	15–23/3/2004	28,414	- SRW - Ontogenetic swimming speeds: max=20 [cm s^{-1}]
5	GoA	Reef polygons (Berenshtein et al., 2017)	Forward	15–23/3/2004	28,414	- CRW: $Kappa_{CRW} = 2.5$ - Ontogenetic swimming speeds: max = 20 [cm s^{-1}]
6	GoA	Reef polygons (Berenshtein et al., 2017)	Forward	15–23/3/2004	28,414	- OVM - CRW: $Kappa_{CRW} = 2.5$ Ontogenetic swimming speeds: max = 20 [cm s^{-1}]
7	GoA	Reef polygons(Berenshtein et al., 2017)	Forward	15–23/3/2004	28,414	- BCRW: $Kappa_{BCRW} = 1$ - Ontogenetic swimming speeds: max = 20 [cm s^{-1}]
8	GoA	Reef polygons (Berenshtein et al., 2017)	Forward	15–23/3/2004	28,414*(14,207)	- Schooling behavior - Ontogenetic swimming speeds: max = 21.4 [cm s^{-1}] - CRW: $Kappa_{CRW} = 4.4$
9	100*100*100 m Sub-sample Centered around 29°29.4′ N 34°57.4′ E	Initial distribution of virtual larvae, with variable patchiness: Lloyds = [1, 6.5, 22, 26, 46] for low larval density (0.0026 ind m^{-3}). And Lloyds = [1, 5.5, 15, 27,38] for high larval density (0.026 ind m^{-3})	Forward	- 15/3/2004 - One releasetracked for 10 mintemporal resolution: 0.1 s	[2,600, 26,000]	Passive

*SRW, simple random walk; CRW, auto-correlated random walk; BCRW, biased correlated random walk; OVM, ontogenetic vertical migration. In all simulations turbulence was applied as a simple random walk (SRW) component (Berenshtein et al., 2017). *For the schooling scenario (#8), the pairs of larvae were moving together by definition. Therefore the effective number of simulated trajectories is half of the released number of larvae.*

Simple Random Walk (SRW)

For this scenario, ontogenetic swimming speeds were applied according to Fisher (2005):

$$u''_t = u''_h + 10^{\frac{\log(t)}{\log(PLD)} \cdot \log(u''_s - u''_h)} \tag{1}$$

Age (t) and PLD are expressed in hours.

Hatching speeds were parameterized with (u''_h) 2 cm s^{-1}, reaching maximum swimming speeds (u''_s) of 20 cm s^{-1}, which are typical values for Pomacentridae (Leis and Carson-Ewart, 1997; Fisher, 2005). Here, the movement directions were drawn from a random distribution, therefore un-correlated and traditionally termed "Simple Random Walk" (SRW). Note, that in all the following behaviors, larval swimming speeds are modeled similarly (Equation 1), with the exception of the passive scenario, were larvae are immobile.

Auto-Correlated Directional Swimming (CRW)

Auto-correlated directional swimming for individual larvae was simulated as a CRW process, such that larval heading at a given time step is correlated to the previous one.

$$\theta_{\mathrm{i}} = \theta_{\mathrm{i}-1} + \delta\theta \tag{2}$$

Where θ_i and θ_{i-1} are the current and previous headings, and $\delta\theta$ is the turning angle, which is drawn from a von-Mises distribution.

$$f(\delta\theta | kappa) = \frac{1}{2\pi I_0(\kappa)} e^{kappa} \tag{3}$$

Where I_0 is a modified Bessel function of order 0, and *Kappa* is the concentration parameter of the von-Mises distribution (Codling et al., 2004; Staaterman et al., 2012; Berenshtein et al., 2017). Briefly, the von-Mises *Kappa* controls the modeled precision of orientation, such that high *Kappa* values would result in directional trajectories, compared to low *Kappa* values. For example, *Kappa* = 0, 2, and 4 will result in a total decay of directional correlation after 10, 100, and 240 min respectively (Berenshtein et al., 2017). *Kappa* values for individual larvae were estimated from the experimental data of Irisson et al. (2015) for the con-familial *Chromis atripectoralis* using maximum likelihood estimation for von-Misses distribution (R core team, 2013) for each headings sequence (i.e., each individual Drifting

In-Situ Chamber experiment). Following this analysis *Kappa* was set to 2.5.

Ontogenetic Vertical Migration (OVM)

The occurrence of OVM was not documented for *N. miryae* but was demonstrated in other pomacentrids, with larvae shown to migrate deeper with age (Paris and Cowen, 2004; Irisson et al., 2009; Huebert et al., 2011). This behavior was implemented in our model (Sim. #6, **Table 1**), such that larvae at the age of 0-5 days post-hatch (DPH) maintained a depth range of 0-25 m, and larvae at the age of 6–27 DPH maintained a depth range of 25-100 m. This is achieved by a vertical movement speed of 2 cm s^{-1}. Larvae older than 27 DPH were within their competence window, and settled to the reef upon encounter.

Biased-Correlated Directional Swimming (BCRW)

Biased-correlated directional swimming for individual larvae was simulated as a biased correlated random walk process (BCRW) such that larval headings are drawn from a von-Mises distribution centered around a pre-defined azimuth; we used 17°, which is the axial direction of the GoA (i.e., larvae that swim toward this direction will end up at the northern tip of the GoA). To date, there is no empirical information about a common swimming directions of larvae in the GoA (in contrast to other locations, e.g., Bottesch et al., 2016), but using the axial direction of the GoA makes biological sense since it minimizes the coastal encounters of the larvae, and therefore minimizes their risk of predation. *Kappa* values for BCRW individual larvae were estimated from the experimental data of Irisson et al. (2015) (see explanation in CRW section above) resulting in kappa = 1.

Schooling Behavior

For schooling behavior, we simulated the most simplified scenario in which pairs of larvae were moving together keeping the exact same positions and paths. Therefore, the effective number of virtual larvae released is half from that of the other strategies (**Table 1**). We have computed the *Kappa* parameter of the von-Mises distribution of turning angles from Irisson et al. (2015) data for the con-familial *C. atripectoralis.* Mean *Kappa* value for CRW computed from that data equaled to 4.4 (see explanation in CRW section above). The mean terminal swimming speed of schooling larvae was set to 21.4 cm s^{-1} which is 7% faster than the individual terminal swimming speed (Irisson et al., 2015).

Passive

In addition the behaviors mentioned above, we have included a passive scenario to provide a baseline for the effect of the various behaviors on the pairwise distances.

Encounter Probability Estimation

For schooling behavior to occur, larvae need to encounter one another. We therefore sought to examine the probability of larvae encountering each other in the pelagic environment soon after hatching (within 1 day).

To address this question, we used two approaches. The first is spatiotemporally explicit, using 3D currents and turbulence from our biophysical model. In the second approach, we use mathematical models modified from the classical planktonic predator-prey encounter rate and probability models (Gerritsen and Strickler, 1977; Kiørboe and MacKenzie, 1995).

Encounter Probability Using the 3D Spatiotemporally Explicit Model

The first approach raised several computational challenges. First, it required a high temporal resolution (<1 s), whereas the temporal resolution of our model is of 10 min. Second, it required realistic densities of larvae, which can be orders of magnitude higher than could be tracked in biophysical models across the entire GoA. Third, to compute all possible pairwise distances across time requires immense computational power.

We therefore created a sub-sample of $100 \times 100 \times 100$ m (length × width × depth) of the GoA, centered around 29°29.4′ N 34°57.4′ E. In this space we followed either 2,600 or 26,000 passive virtual larvae, which correspond to the lower and mid-level values of measured densities of the con-familial *Stegastes partitus* larvae (<6 DPH, Paris and Cowen, 2004). The larvae, were released on the 15th of March 2004 at 12:00 p.m., and tracked for 10 min at a temporal resolution of 0.1 s. Initial positions of the passive larvae were generated at levels of patchiness [Lloyd's index of patchiness (L); (Lloyd, 1967)] that ranged from random distribution ($L = 1$) to moderately clumped ($L = 40$) distribution (Bradbury et al., 2003).

Random distributions were generated by selecting random XYZ coordinates within the cubic domain. Clumped distributions were generated using an iterative algorithm which produced the initial positions of virtual larvae around predefined number of centroids ($Np_1 = 20$), randomly drawn from a uniform distribution within a pre-defined distance ($Rp_1 = 20$ m) from a given patch centroid. For each iteration, to compute Lloyd's index of patchiness, 100 samples ($7 \times 7 \times 7$ m) were randomly placed in the domain. Then Np_i and the Rp_i were iteratively modified until reaching the desired range of patchiness. The sample's volume (343 m^3) is within the range of typical ichthyoplankton samples (Kimmerling et al., 2017). Visualization examples of the spatial patterns are presented in Supplementary Figure S1.

We assumed a detection distance of 0.1 m, which corresponds to the visual acuity in fish larvae (Renee Lara, 2001). Encounter probability was computed as the proportion of larvae, out of the total number released, that came within 0.1 m of at least one other larvae throughout the 10 min simulation.

Encounter Probability Using the Classic Encounter Model

For the classic approach we used the encounter rate model from Kiørboe and MacKenzie (1995) between planktonic predator and prey. Here the encounter rate (*Er*) was a function of larval density (*D*; using 0.026 and 0.0026 ind m^{-3}), detection distance (*R*; using 0.1 m), and swimming speed (*v*; using values of 0 and 0.02 m s^{-1}; Fisher, 2005).

$$Er = \pi D R^2 \sqrt{(2w^2 + 2v^2)} \tag{4}$$

Turbulent velocity (w) was computed following Kiørboe and MacKenzie (1995), using turbulent dissipation rates (ε) of 10^{-7} and 10^{-4} m^2 s^{-3} which represent the range of turbulent dissipation rates for the shelf and coastal zones (Kiorboe and Saiz, 1995).

$$w = 1.9(\epsilon \mathrm{R})^{1/3} \tag{5}$$

Encounter probability was computed following Gerritsen and Strickler (1977), where encounters were assumed to be randomly occurring events (Poisson distribution). Therefore the probability encountering at least one larvae (P_E) was formulated as a function of the time interval (t; using 10 min and 24 h).

$$P_E\,(\Delta t) = 1 - \, e^{-Er\Delta t}\frac{(Er\Delta t)^0}{0!} = 1 - \, e^{-Er\Delta t} \tag{6}$$

The term e^{-Ert} in Equation (6) represents the probability encountering 0 larvae.

Assessment of the Capacity of Newly Hatched Larvae to Overcome Turbulence and Remain Grouped

To assess the capacity of adjacent larvae to overcome horizontal turbulence and stay grouped, we computed turbulent velocity using Kiørboe and MacKenzie (1995) approach (Equation 5), and compared it to the combined velocity of two larvae swimming one toward the other.

Assessment of Grouping Tendency From Kimmerling et al. (2017) Data

The grouping tendency of *N. miryae* and *Chromis viridis* was assessed using the sampling data from Kimmerling et al. (2017). We focused on these two species as they were the species examined in Ben-Tzvi et al. (2012), with *N. miryae* demonstrating cohesive dispersal pattern, while *C. viridis* did not. The frequency and number of individuals occurring in the ichthyoplankton samples was recorded, and their Lloyds Index of Patchiness was computed.

Settlement Success and Connectivity Network Density

Settlement-success was computed as the percent of virtual larvae that have reached a reef polygon within their competence window (last 48 h of their PLD; Berenshtein et al., 2017). Network-density was computed as the percent of realized connections out of all possible connections between the different polygons in the GoA domain. Network-density considered only whether or not connections occurred, without considering the connections strength.

Settlement success and network density were computed per release event ($N = 9$; Sim #5 and #8, **Table 1**). Paired t-tests were used to examine the significance of differences in terms of settlement-success and network-density between schooling vs. individual CRW larvae. Shapiro-Wilk test was used to examine the normality of the paired differences. All simulations and statistical analyses were run on MATLAB R2014b (The MathWorks Inc., Natick, MA, USA) and R (R core team, 2013).

RESULTS

Backward and Forward-in-Time Passive Simulations

Backtracking of passive virtual larvae from the sites and times of settlement by *N. miryae* (**Figure 2A**) resulted in a wide spread of trajectories around the northern two-thirds of the GoA; with a high degree of overlap between cohorts (**Figure 2A**). Similarly, forward-in-time trajectories, released from reef sources from the backtracking simulations, did not show any channeling patterns toward the observed settlement sites, but instead were widespread across most of the GoA area (**Figure 2B**). Both backward and forward in-time trajectories showed no evidence for prevailing currents that could generate cohort cohesion (Ben-Tzvi et al., 2012).

Pairwise Distances and Probability of Adjacent Settlement

The analysis of pairwise-distances indicated that all but the schooling scenarios resulted in a high degree of dispersion. Mean pairwise distances at the end of the PLD ranged between 13 and 38 km, for pairs of larvae that hatched at the same location and time (**Figure 3**). Behaviors which include movement toward similar horizontal or vertical directions among larvae (BCRW and OVM) resulted in path convergence in comparison to the passive scenario, while dispersive behaviors which lacked "common movement direction" (SRW and CRW) resulted in greater path divergence in comparison to the passive scenario. Yet, even for the most convergent scenario (BCRW), the pairwise distances were far from generating patterns of cohesive dispersal, i.e., cohort members that settled within a few meters one from another (Ben-Tzvi et al., 2012). By definition, pairwise-distances under the schooling behavior scenario equaled zero. All behaviors are characterized by a nearly linear increase of pairwise distances with slopes slightly decreasing toward the end of the PLD due to the bounded domain of the GoA. An exception is BCRW, which shows a considerably earlier and steeper decline in the pairwise distances due to convergence of larvae toward the northern tip of the GoA.

Similarly, the probability of sampling a nearest neighbor pair which hatched at the same location and time for all but the "schooling behavior" strategy was extremely low (<0.00004). Naturally, in the schooling behavior scenario, as the larval pairs hatched, moved, and settled together, the probability for pairwise settlement is maximal.

Larval Encounter Probabilities

The probability of larval encounter per 10 min, from the 3D biophysical model, ranged between 0.0046 and 0.49 at low larval densities, and 0.046-0.78 at high larval densities, depending the degree of initial larval patchiness (**Figure 4**; for spatial distribution see Supplementary Figure S1).

Encounter probabilities computed with the classic encounter model (Kiørboe and MacKenzie, 1995) ranged from 0.001 to 0.99

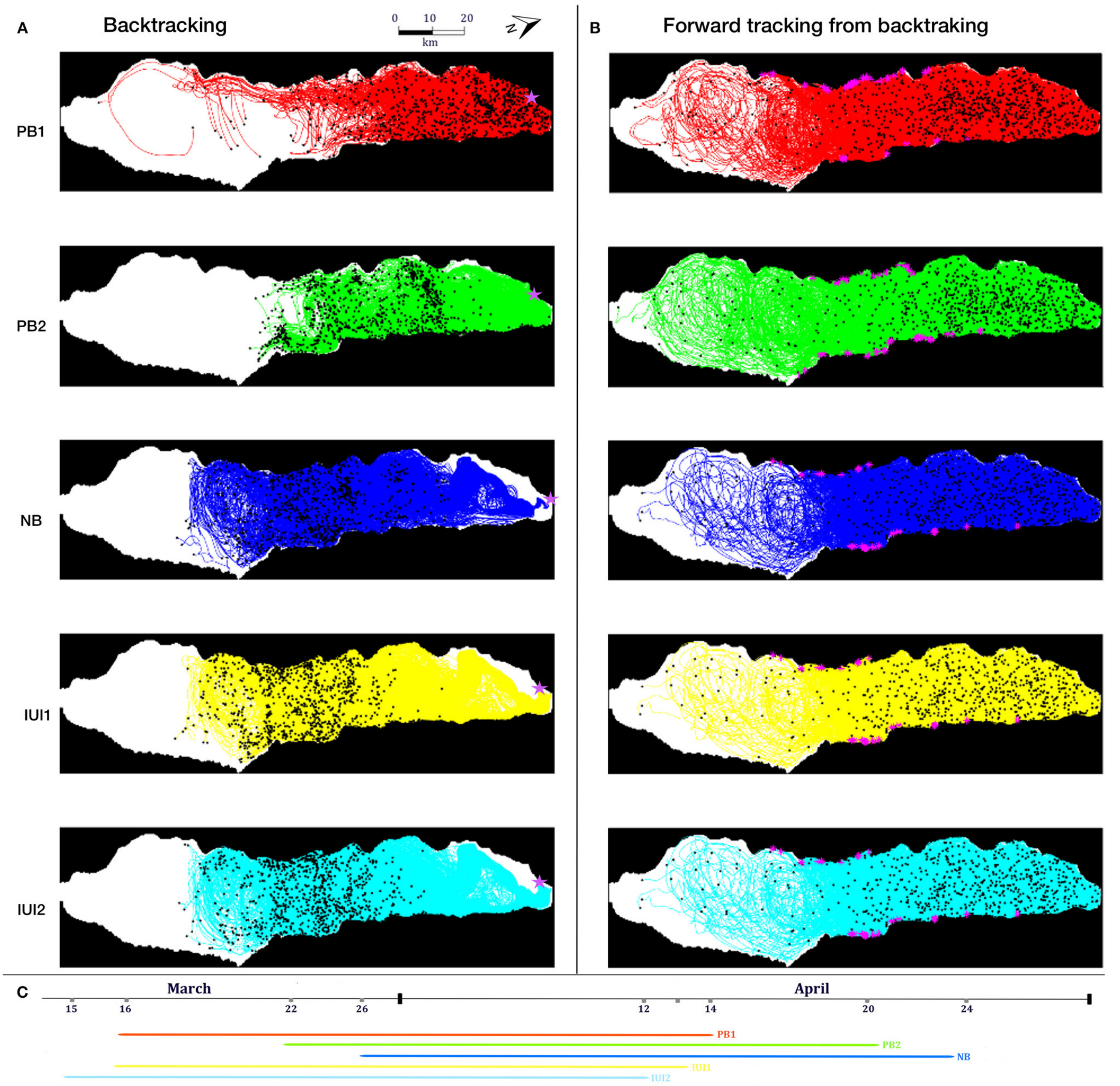

FIGURE 2 | **(A)** Trajectories of passive virtual larvae released at the locations and times of settlement (*n* = 5,000 per site) and tracked backward in time for a duration of 28–29 days (Sim. #1, **Table 1**). Virtual larvae from **(A)** with final positions in the reef (*n* = 244) were multiplied (×20) and tracked forward in time for 28–29 days **(B)**. Magenta asterisks in **(A,B)** represent particle release locations. **(C)** Pelagic Larval Durations (PLD) of the recruiting cohorts from April-March 2004, which were deducted from otolith analysis in Ben-Tzvi et al. (2012). Maps in **(A,B)** were generated using MATLAB R2014b (The MathWorks Inc., Natick, MA, USA), and are rotated views of the GoA (73° Clockwise).

depending on larval density, time span, turbulent velocity, and swimming speeds (**Table 2**). Across 24 h, for high larval densities, the encounter probability of swimming larvae is 0.2 and 0.99 for low and high turbulent dissipation rates respectively (**Table 2**, Supplementary Figure S2). Increase in larval density, time span, turbulent velocity, and swimming speeds resulted in an increase in encounter probabilities.

Assessment of the Capacity of Newly Hatched Larvae to Overcome Turbulence and Remain Grouped

Computation of turbulent velocity (Equation 5) for dissipation rate of 10^{-4} m^2 s^{-3} resulted in a turbulent velocity of $w = 0.041$ m s^{-1}. Given maximal larval speeds during the first 24 h after hatching is 0.02–0.03 m s^{-1}, larvae that swim toward

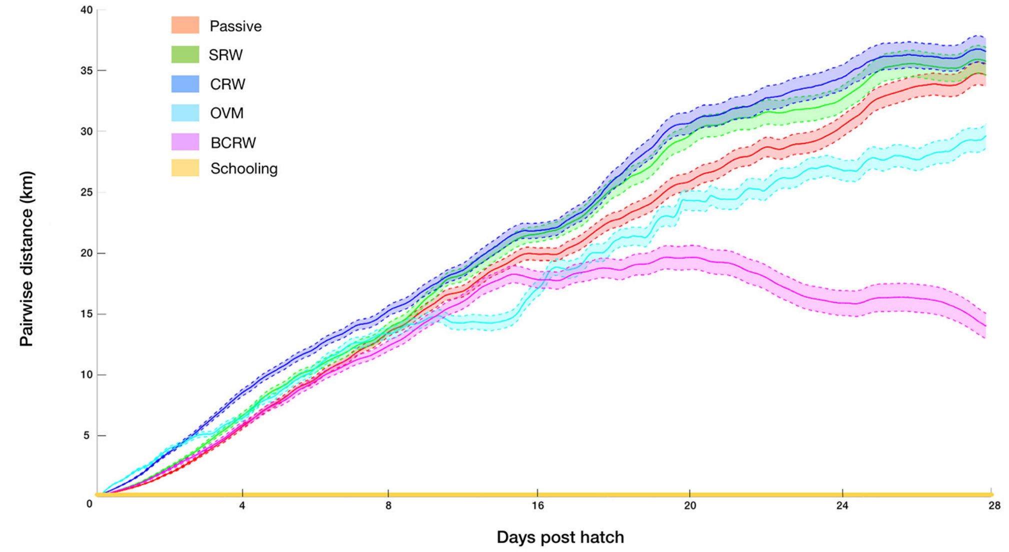

FIGURE 3 | Distances between pairs of virtual larvae that hatched at the same locations and times throughout the pelagic larval duration (PLD) for the following strategies: passive, simple random walk (SRW), auto-correlated directional swimming (CRW), ontogenetic vertical migration (OVM), biased correlated random walk (BCRW), and schooling behavior (simulation #3–8, **Table 1**). Shaded areas indicate 99% confidence intervals ($N = 32{,}046$ and 28,414 for the passive and other strategies respectively).

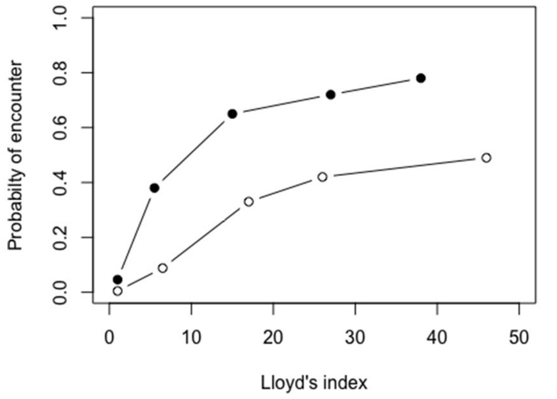

FIGURE 4 | Encounter probabilities of passive larvae as a function of the patchiness of initial larval distribution, implementing high (0.026 ind m^{-3}; full circles) and low (0.0026 ind m^{-3}; empty circles) larval densities. Simulations were carried out in the 3D biophysical model within a sub-sample of 100 × 100 × 100 m (length × width × depth) in the Gulf of Aqaba centered around 29°29.4′ N 34°57.4′ E during the 15th of March 2004 at 12:00–12:10 p.m.

each other would be able to overcome turbulent velocity and remain grouped. Dissipation rate of 10^{-4} m^2 s^{-3} represents the upper limit of coastal and shelf dissipation rates, suggesting that such larvae, which can swim since hatching, will be able to overcome turbulent velocity and remain grouped at nearly all oceanic conditions, from early stages of their PLD.

Assessment of Grouping Tendency From Kimmerling et al. (2017) Data

For *N. miryae*, 90% of the samples contained two or more larvae, compared to only 29% in *C. viridis*. Lloyd's index of patchiness for *N. miryae* was 64 compared to 27 for *C. viridis*.

Settlement Success and Connectivity Network Density

Settlement success of schooling larvae was significantly higher than that of non-schooling larvae (pairwise *t*-test, $t = 26.3$, $df = 8$, $p < 0.01$, **Figure 5**). Connectivity network density in schooling larvae was significantly lower than that achieved in the non-schooling scenario (pairwise *t*-test, $t = -35.2$, $df = 8$, $p < 0.01$, **Figure 5**).

DISCUSSION

Of the simulation scenarios considered in the current study, patterns of cohesive dispersal could only be reproduced by schooling behavior (**Figure 3**). This would seem to suggest that newly hatched *N. miryae* may actively form long-lived schools.

To school, larvae must encounter one another, yet schooling does not seem to occur immediately after hatching for the following reasons: (1) There is no indication for synchronous hatching from Pomacenridae demersal eggs, (2) There is no genetic structure between larval cohorts (Ben-Tzvi et al., 2012), and (3) Larval swimming velocities at hatching are not necessarily sufficient to overcome turbulent velocity. Therefore, *N. miryae* encounter their conspecifics shortly—but not immediately—after hatching.

The larval encounter analyses computed in this study demonstrated feasible probabilities for pelagic larval encounter within 24 h (**Table 2**, **Figure 4**). However, both encounter computation methods encompass some limitations. The mathematical model assumes larval distributions are random rather than clumped. The latter has been documented for fish larvae (e.g., Bradbury et al., 2003, $L>3$; Frank et al., 1993, $L>2$), and for later-stage larvae of *N. miryae* in the GoA (Kimmerling

TABLE 2 | Sensitivity analysis of larval encounter rates and probabilities as a function of larval density, time span, larval swimming speeds, and turbulent velocities.

Density (larvae m^{-3})	Time span (s)	Swimming speed (m s^{-1})	Dissipation rate (m^2 s^{-3})	Turbulent velocity(m s^{-1})	Encounter rate (s^{-1})	Encounter probability
0.0026	600	0	10^{-7}	0.004	4.73×10^{-4}	0.000
0.0026	600	0.02	10^{-7}	0.004	2.36×10^{-6}	0.001
0.0026	600	0	10^{-4}	0.041	4.73×10^{-6}	0.003
0.026	600	0	10^{-7}	0.004	4.73×10^{-6}	0.003
0.0026	600	0.02	10^{-4}	0.041	5.26×10^{-6}	0.003
0.026	600	0.02	10^{-7}	0.004	2.36×10^{-5}	0.014
0.026	600	0	10^{-4}	0.041	4.73×10^{-5}	0.028
0.026	600	0.02	10^{-4}	0.041	5.26×10^{-5}	0.031
0.0026	86,400	0	10^{-7}	0.004	4.73×10^{-7}	0.040
0.0026	86,400	0.02	10^{-7}	0.004	2.36×10^{-6}	0.184
0.0026	86,400	0	10^{-4}	0.041	4.73×10^{-6}	0.335
0.026	86,400	0	10^{-7}	0.004	4.73×10^{-6}	0.335
0.0026	86,400	0.02	10^{-4}	0.041	5.26×10^{-6}	0.365
0.026	86,400	0.02	10^{-7}	0.004	2.36×10^{-5}	0.870
0.026	86,400	0	10^{-4}	0.041	4.73×10^{-5}	0.983
0.026	86,400	0.02	10^{-4}	0.041	5.26×10^{-5}	0.989

Encounter rates and turbulent velocities were computed according to Kiørboe and MacKenzie (1995), and encounter probabilities were computed according to Gerritsen and Strickler (1977), for larval encounter with at least one other larva. Rows are sorted according to increasing encounter probabilities values. For graphical representation of this data see Supplementary Figure S2.

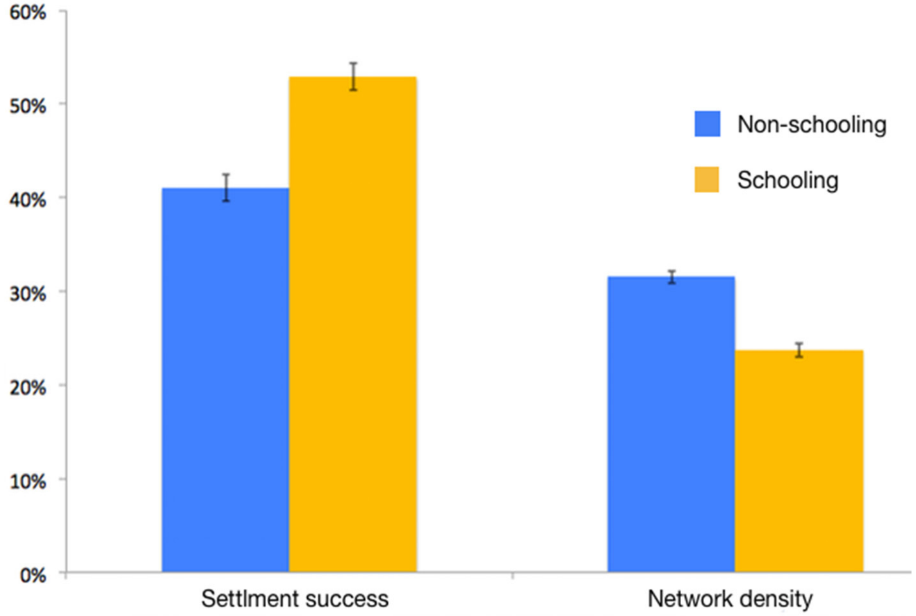

FIGURE 5 | Settlement success and connectivity network density (i.e., the percentage of realized connections out of all possible connections) of individual and schooling larvae (Sim. #5 vs. #8 in **Table 1**).

et al., 2017, L = 64). The 3D—spatio-temporally explicit model is limited as well, since advection, and turbulence transport the larvae away from their initially confined cubic domain to waters which are empty of larvae. This alters the shape and the volume of the waters encompassing the larval patch, resulting in a modification of the effective densities across time. Despite these limitations, both methods indicate that larval encounter within the first 24 h post-hatching can be feasible.

Even when larvae encounter each other they still need to overcome turbulent velocity to keep together. The fact that larval swimming velocities soon after hatching were similar to the upper range of turbulent velocities (Dissipation rate of 10^{-4} m^3 s^{-2};

Table 2) suggests that fish larvae can maintain schooling in most oceanic conditions.

To keep together, larvae may utilize their vision and lateral line senses similarly to adult fish (Partridge and Pitcher, 1980), and their olfactory sense similarly to settlement stage larvae (Lecchini et al., 2014). They may also use their auditory sense, as fish larvae can produce sounds during the night (Staaterman et al., 2014).

The fact that larvae within cohorts stayed together through their PLD (Ben-Tzvi et al., 2012) suggests a high cohort fidelity and a lack of (or little) mixing with other cohorts or sporadic individuals (i.e., cohesive dispersal). This, in turn, suggests that *N. miryae* larvae would form scarce and clumped patches in the pelagic environment.

The spatial scale of cohesive dispersal is unknown due to the limited information about the spatial heterogeneity of trace-elements used in Ben-Tzvi et al. (2012). However, using the available information, we can make a simplistic assessment of the spatial extent of newly formed cohorts, which results in length scales of tens to hundreds of meters (Supplementary Data S1). At these small scales, convergent oceanographic features, which could potentially aggregate larvae but are too small to be resolved by the MITgcm model, could occur (e.g., Gildor et al., 2009). Yet, such features are rare and persistent across no more than a few days, and therefore cannot produce the observed cohesive pattern across the PLD (Ben-Tzvi et al., 2012).

Schooling behavior, along with other biological and physical factors (e.g., Fronts, pycnoclines, and heterogeneous distribution of larva predator and prey) can contribute to larval patchiness (e.g., McGurk, 1986; Frank et al., 1993). Ichthyoplankton samples from Kimmerling et al. (2017) suggest a stronger tendency of *N. miryae* to be found in groups compared to *C. viridis,* whose otolith analysis lacked any evidence for cohesive dispersal (Ben-Tzvi et al., 2012). Note however, that the larvae of these two species are characterized by different spatio-temporal dynamics which may also effect their tendency to be found in groups (Kimmerling et al., 2017). Naturally, Interplay between biological and physical factors can effect schooling dynamics, as more patchy populations have a higher probability of encounter, and therefore facilitate schooling.

Previous studies demonstrated that the extent of patchiness often follows a "U" shaped curve across ontogeny (for example in Capelin and Sandlance larvae/eggs; Bradbury et al., 2003). Initial high patchiness is attributed to the coherence of larvae/eggs patches from mass-spawning/hatching at specific areas; the following decrease is attributed mainly to advection and mortality; and the increase toward the end of the PLD is attributed to active larval behavior (Bradbury et al., 2003). While Frank et al. (1993) attributed that increase to the occurrence of prey (*Sagitta elegans*), schooling behavior may have also played a role in these dynamics.

In our current biophysical model, mortality was not applied. In other modeling efforts, mortality is mostly applied as a constant rate in time and space due to limited empirical information. Such application of mortality is not expected to effect the results and the conclusions of this study (e.g., Berenshtein et al., 2017).

Increased schooling capacity can affect fitness both positively and negatively. Positive effects include increased swimming speeds and orientation capacities (Irisson et al., 2015), which are manifested in increased settlement success (**Figure 5**; Berenshtein et al., 2017); while negative effects may include higher probability of predator encounter due to increased mobility (swimming velocity and directional persistence; Visser and Kiørboe, 2006), increased competition for food, and the reduction of variation in effective dispersal paths (i.e., connectivity; **Figure 5**).

The increased settlement success of schooling larvae is attributed to higher swimming speeds and a more precise orientation (Irisson et al., 2015), which lead to an increase in displacement associated with larval behavior (Berenshtein et al., 2017). This, in turn, allows the larvae to depart from entraining currents (e.g., sub-mesoscale eddies) and increases their probability of reaching the coast and settling (Berenshtein et al., 2017). The decrease in connectivity network density (**Figure 5**) is attributed to the reduction of the variation in dispersal trajectories. In other words, a population of larvae which disperses in pairs for example, can produce half of the dispersal paths generated by individually dispersing larvae.

These changes in settlement success and connectivity are important as these factors are central in population dynamics, affecting the biogeography and the genetic structure of populations in multiple marine species (Cowen and Sponaugle, 2009). Moreover, larval supply from external (non-local) sources is essential for sustaining populations, i.e., sites which receive larvae from multiple sources would be less susceptible for a population collapse compared to sites which are dependent on fewer sources (Cowen et al., 2006).As schooling in fish larvae might be very common (reviewed in Leis, 2006), *in-situ* and laboratory studies are needed to examine ontogenetic larval collective behavior, and specifically their fission-fusion dynamics across their PLD. This, in conjunction with ichthyoplankton analyses of species abundances throughout ontogeny, could set the basis for a realistic incorporation of schooling behavior in biophysical models.

In conclusion, this study supports the occurrence of schooling of *N. miryae* in the GoA across the PLD for realistic reconstruction of observed settlement patterns. In addition, our study demonstrates the effects of schooling behavior on larval settlement success and connectivity. The dynamics and characteristics of larval schooling should be further studied, and its application should be considered in larval dispersal models when managing fisheries and determining marine protected areas.

AUTHOR CONTRIBUTIONS

IB, HG, YA, EF, and MK participated in data analysis, EF adjusted and run the atmospheric model, and helped with the particle tracking algorithm, HG and YA adjusted and run the oceanographic model, IB, CP, and MK participated in conceiving, designing, and drafting the study.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2018.00254/full#supplementary-material

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